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BIOLOGY OF DESERTS

THE PROCEEDINGS OF A SYMPOSIUM
ON THE BIOLOGY OF HOT AND COLD DESERTS
ORGANIZED BY THE INSTITUTE OF BIOLOGY

EDITED BY J.L.CLOUDSLEY-THOMPSON

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FOREWORD

This volume contains papers read at a Conference on 'The Biology and Productivity of Hot and Cold Deserts', organised by the Institute of Biology, and held at the Royal Institution during September 25th, 26th and 27th, 1952. The Symposium consisted of six sessions devoted to various aspects of desert biology as follows:-

I Climate and Physical Environment

II Plant Ecology

III Entomology and Ecology

IV Economic Aspects

V Mammalian Physiology and Ecology: I

VI Mammalian Physiology and Ecology: II

It was opened by Dr Edward Hindle, F.R.S. President of the Institute. In welcoming delegates from abroad, Dr Hindle mentioned that the United Nations Educational, Scientific and Cultural Organisation had shown a special interest in the conference, and had contributed toward the travelling expenses of speakers from oversea. A meeting of the Unesco Arid Zone Committee took place immediately after the symposium.

Most of the papers were naturally concerned with the scientific problems involved in attempts to increase the productivity of deserts and arid zones to meet the ever increasing needs of a hungry world. A synopsis of some of the chief topics mentioned in the various discussions has been provided.

The publication of this volume has been assisted by a grant from Unesco. The Council of the Institute of Biology wishes to record its gratitude to Unesco for this assistance.

The Editor would like to extend a personal appreciation to Mr D. J. B. Copp, General Secretary of the Institute of Biology and to Mr C. A. Ronan and Miss T. J. Tippett of the Secretariat of the Royal Society.

J. L. Cloudsley - Thompson
Editor.

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CONTENTS

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THE GEOGRAPHY OF DESERTS

Professor Frank Debenham O.B.E.

(*Cambridge*)

This paper, being introductory to a series which deals with special aspects of deserts, can be little more than a review of where deserts occur on the world's surface and why, with some reminders of how many and varied are the factors which may combine to produce a desert.

In broadest outline the origin of an arid zone on land is simple enough, since it is caused by an interruption or suspension of the exchange of water from sea to land via the air in a certain area. They are in fact due to flaws in the fundamental cycle on which all life on land depends, the cycle which raises water by evaporation from the sea, against gravity, moves it over the land, where it is precipitated, and then, in part, brings it back to the sea again by gravity.

The primary factor in the distribution of deserts is therefore the scheme of world circulation of air, since an on-shore wind can bring water from sea to land whereas an off-shore wind cannot. On the continental scale, indeed, arid zones must occur on the lee side of the land with respect to the prevalent winds.

That appears at first sight to be a neat explanation of the occurrence of deserts on the western side of continents in the southern hemisphere round about the latitude of the Tropic of Capricorn, but by itself it is by no means an adequate one. It leaves out of account at least two major factors — first, the temperature of the sea which is to yield the water as vapour and, second, the seasonal swing of the zone of Equatorial pressure, which together with the polar areas appears to govern the circulation of the atmosphere.

The temperature of the sea, again, is dependent on ocean currents, themselves mainly due to prevalent winds far away from the actual arid zones. These, in the comparatively simple set of circumstances of the southern hemisphere, tend to bring warm equatorial water to the eastern sides of the continents and cold polar water to the western sides.

Added to that component we must note too that a continuous off-shore wind tends to bring up cold bottom water to the surface of the sea, while an on-shore wind piles up warmer surface water against the land. The cold water will extract water vapour from the air in the form of fogs and mists, while the warm water on the other side will give itself up to the atmosphere.

The argument as to the origin of arid regions is already becoming complicated, yet we have not mentioned several other factors which must bear on the matter, such as the distribution of the land masses, the topography of the land itself, and the incidence of those enormous eddies in the atmosphere which we are accustomed to call 'depressions' and which appear to upset the neat pattern of world circulation of air in both plan and elevation. It might be wise therefore to leave the argument at that point and view the occurrence of deserts from another and simpler angle.

An arid region is one where the precipitation is much less than the world average and therefore where the amount of water as vapour in the air is much less than the average also. This state of affairs can come about in two ways – either the air has lost the water it originally had or else it never had a very good supply. To put this in a more scientific way, the air over an arid region is far below saturation point, and it may reach that state because its temperature has been raised after losing its original supply or because its original temperature was low and therefore it never had a good supply.

We may illustrate this by referring to the conditions on that narrow but very extreme desert of the Namib which stretches along the coast of South-west Africa for hundreds of miles. In the rainy season for Southern Africa, roughly from November to March, the easterly winds from the Indian Ocean bring warm and nearly saturated air inland. Forced up over the Drakensberg range and the plateau behind it is cooled and parts with much of its vapour as rain. When it reaches the so-called Kalahari Desert it still has enough vapour to produce some thunderstorm rain, and if it does not fall there it will fall further west where the higher land of South-west Africa cools it. The air then descends to the coast and warms up as it goes so that at sea-level it is so far below saturation point that even the cold Benguela current can only produce an occasional fog.

At other times of the year there are occasional drifts of air from the Atlantic inland over the Namib, but it has come from the cold surface current and again is so far below saturation point that it cannot do better than an occasional mist. We should note that this fogginess may be, and in the Namib often is, a very important factor for the biology of that area; but nevertheless it remains a very severe desert.

We may therefore think of most deserts as largely due to their occupying vast areas of rain-shadow, that is to say, areas which are on the lee side of land which has robbed the air of most of its precipitable moisture. Narrow coastal deserts such as those of South-west Africa and Chile add the effect of a cold current off-shore and are more arid still. This simple explanation of the distribution of deserts will, no doubt, be amplified by papers later in this symposium.

Yet no desert is completely and permanently without water, just as the air above it is never completely dry, and it is as well that biologists should realise just how moisture does reach the ground to sustain such desert life as exists.

Dry air means clear skies and clear skies mean excessive insolation by day and radiation by night – the two processes which are mainly responsible for some degree of precipitation. The rapid heating of the land by the sun by day induces rising currents of air, which are usually local in extent. On the smaller scale these produce the familiar dust-whirlwinds which have so many curious names in different parts of the world. On the larger scale these upward currents will take the air high enough to cool down by adiabatic expansion and even reach dewpoint, so that clouds are formed – usually of the cumulus type, since the release of heat within them still further accelerates the rate of ascent of air. These often produce rain, as their fuzzy under-surfaces show, but it is rain which rarely reaches the ground, and indeed one can see it

evaporating in wispy tails to the clouds as it descends. When it does reach the ground it tends to be torrential and brief, the thunderstorm type, and comparatively local in extent.

Thus the two characteristics of desert rainfall are that it is accidental, being due to a disturbance of equilibrium in the air, and that it is usually local in extent. In the tropics it tends to be seasonal, precisely because the desert is in a rain-shadow area and the air reaching it during the rainy season to windward is at least more saturated than at other times of the year.

Returning to the heavy insolation which is the cause of this instability rainfall, we must note that it is much more effective on dark bare soil than on light-coloured soil with some vegetation covering. This fact appears to me to be of considerable importance in the biology of deserts, though of course it applies rather to the semi-desert where vegetation cover can occur than to the utter desert where it cannot.

In the western and drier parts of the Kalahari, for instance, the cover of low bush and grass is quite considerable in the so-called rainy season. On the 'pans' however, which tend to occur in chains, the ground is either bare because of its salt content or has a short grass, kept shorter still by the herds of springbok. It was noticed during my visit there that the thunderstorms tended to keep to the pans, that is to the centres of the rising air currents. On one particular day a series of over a dozen heavy thunderstorms passed along such a line of pans. At our camp, situated on a sand-ridge half-a-mile from this chain, only one of the storms produced rain, though it was nearly half-an-inch in half-an-hour. The natural deduction was that over the pans the rainfall that day was very much greater, possibly several inches. This deduction was supported by the fact that the next day our lorries were badly bogged crossing one of these pans, over which two days before we had driven at speed.

In any area of instability rainfall we have to be very cautious about accepting rain-gauge data, but it will be doubly so if there is ground for suspecting that storms choose their paths with some consistency, in the way outlined above.

If the tremendous insolation by day in a desert causes great vertical disturbance in the atmosphere, the opposite occurs at night. The rapid cooling tends to cause an inversion of temperature, so that air in contact with the ground becomes heavier and remains there. All desert travellers are familiar with the experience of insupportable heat by day and desperate cold at night. It is no exaggeration to say that a basin of water outside one's tent may be frozen at six in the morning, thawed by eight and at blood temperature by noon.

These rapid changes of temperature must obviously affect plants and animals in the desert, but at the moment we are concerned chiefly with the yield of moisture so caused. Measured in inches, even if that were possible, the total derived from frost-rime and dew would not be impressive, but the fact that it is in immediate contact with leaves and branches is no doubt of biological significance. Certainly it is the case that some antelope, notably the springbok, derive all their water-supply from the dew on the grass in the early morning. Later papers will perhaps assess the value of this source of moisture, particularly in the case of plants.

We come now to a very vital problem in the physical geography of deserts, namely, what becomes of such rain as does fall. The data we have on this important aspect of arid areas are still very incomplete, nor have they been collected into any general summary so far as I know. We know little as to the relation between evaporation, run-off and absorption in deserts, which is hardly to be wondered at for not only are stations suitable for such observations very rare but the number of factors involved is so large that data can rarely be of general application. It goes without saying that evaporation must be high and that run-off on loose sand must be low or non-existent. It is the remaining proportion which is so important and so difficult to measure.

We cannot here become involved in the figures available from French engineers in North Africa, American engineers from work in their drier states, and British workers chiefly in India, since they do not mean very much without accessory observations of a very local kind such as the nature of the ground, the rate at which the rain falls, the temperature of air and ground, the wind, and even the time of day. All we can say is that in most deserts there is some portion of the rainfall which succeeds in passing through the upper layers beyond the reach of plants, there to form a water-table which will appear as seepage springs in an oasis or can be tapped by bores. Much of it may remain in partially enclosed areas underground, to become brackish and to cement the sand grains into a calcrete or a silcrete. The term 'fossil water' has been used for such occurrences but it is not a very useful phrase. Obviously there must be critical points as to the amount of rain, its rate of fall, and the other factors mentioned, below which no water is conserved beneath the surface, and this critical point will vary with each desert and again at different places within that desert.

It seems likely that the most critical factor may well be the rate at which rainfall can seep downwards through the sand and soil, since it is a question of a race between capillary action taking it back towards the surface and gravity leading it downwards, beyond the reach both of plant roots and of the capillary rise, and the issue of the race is largely dependent on the porosity. An accessory factor may be the imprisonment of air below the sodden layer after a storm; at least, that was my interpretation of an observation we made in the northern, wetter, portion of the Kalahari. We were boring with a hand-sampler, which in this case took us down 20 feet, and it was in the middle of the rainy season. The first 3 feet produced damp, not saturated, sand and then we suddenly ran into 10 feet of perfectly dry sand. At about 13 feet the sand was again damp, and so continued to the limit we reached. From a nearby bore the water-table here was at 40 feet. We took it that the zone of dry sand represented the previous dry season and were surprised that six weeks of a rainy season, which on average should have yielded about 8 inches, had here penetrated to only 3 feet. It was the usual fine yellow Kalahari sand, which by experiment absorbed water at a much greater rate than that.

An isolated observation of that kind is of little value, but nevertheless one seeks for an explanation, just as one wonders how the reservoir at 40 feet or so can get any significant replenishment each year under such a régime.

The hydrology of deserts must sound to the layman like a contradiction in terms, yet it is the study of a desert's water-supply which is the basis of this whole con-

ference, since it is essential to all forms of life. It follows that the only absolute desert from the biological point of view is that which has no reserve of water, no means by which the rare rainfall can escape from instant evaporation. From that aspect the boulder-strewn rocky surfaces of the Sahara or of the Australian Central Desert are more nearly absolute in their aridity than the moving sand-dunes, for the latter will at least store rain within their mass, letting it our slowly to keep alive those scant bushes in the troughs between the dunes.

This brings us to what, as a geographer interested in the practical application of scientific knowledge, I regard as the most important consideration to come before the participants in this conference. Even though deserts are, at the very best, but marginal land for the use of man, it behoves us to make what use we can of them. That use, as we know, depends on the available reserves of water, but the investigation of what reserves there are, is at present, a very expensive business.

Yet we know there must be some close relation between the available water and those plants which are permanent occupants of an arid area, and they must therefore be indicators in some degree of the underground water. The ecologist and the physical geographer have the duty of finding out how far one can trust indicator plants, which, after all, are best qualified to give us the information once we have wit to interpret their message.

In the past when searching for sub-surface water in arid areas we have been accustomed to send water-engineers and geologists and even physical geographers. In my opinion the ecologist is the more appropriate scientist for such a mission, since he should be able to ask the question of the plants, which really do know the answer, whereas the rocks and the sand carry no visible proof that there is water below the surface.

To conclude on a still more practical note, I would suggest that the biologists equip themselves more fully for this new duty by field-work directed especially to finding out more about such indicator plants, particularly in those semi-arid regions which could be put to better use than they are at present. I should like to quote the particular case of my own favourite 'desert', so miscalled, the Kalahari.

Even in the worst parts of it there is a cover of bushes and small trees which survive one- or two-year droughts. To prove by drilling that there are underground water supplies would be a costly and haphazard means of investigation. I would rather employ a field ecologist who would make it his chief if not his sole purpose to establish a relationship between sub-surface supplies of water and perennial plants.

The whole secret of life in arid regions is movement, a readiness and a freedom to migrate. This is obvious enough for man and the larger animals who somehow find out where the casual storms have occurred and move to the pastures so benefited. For the less mobile small fry and the immobile plants it is a case of adapting themselves to endure long dry periods in a state of dormant or suspended animation. This they do in a myriad different ways, and perhaps the best examples of adaptation to environment are to be found in deserts. These adaptations however are in delicate balance and it is for the biologist to study how far it is safe for man to interfere with them for

his own benefit. A very obvious example is the replacement in some Middle East arid districts of the migrant gazelle, which only nibbles thorn-bushes, by the goat, which eats them to the ground.

If semi-deserts are to become free ranching grounds the greatest care will have to be taken as to stocking well below capacity, moving the cattle constantly, and useing the principles of pasture management.

In the meantime the scientist, and particularly the biologist, must find out a great deal more about desert ecology and the correlation between the water resources and the indigenous flora.

THE PHYSICAL ASPECTS OF DRY DESERTS

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(*London*)

Cause and General Character of Dry Deserts

A desert can be defined as a region where the physical conditions are adverse to human ecology, beyond some agreed stage. But there is no reason to confine ourselves to human economy, and in any case we ought to think of the economy of desert folk rather than of western civilisation. This kind of definition would be all right if the physical conditions were uniform from one area of the region to another and from year to year. But they are not. Hence for the proper study of the biology and productivity of deserts we must have a clear idea not only of the general physical factors but also of their variation from place to place and from year to year.

In what follows I shall include the more arid and the less economically inviting desert conditions because I feel one can often see a particular important but narrow part of a wide range of conditions in far better perspective after having seen the extremities of the range. And unfortunately very few biologists have had personal access to the arid extremity. If I shall sin at times as a layman by straying into the realm of biology, it will be for the same reason.

The primary cause of the great sub-tropical deserts is quite clearly meteorological, though it is not heat but lack of moisture. Life can thrive in the very hottest spots known. Desert regions lie beneath more or less permanent anticyclones where the dry upper air descends to the ground. Atmospheric moisture is therefore low, rainfall is slight and precarious. The sun's radiation is for long periods unshielded by cloud. Summer day temperatures are high. The downward seepage of water through the sub-soil is so infrequent that salts tend to rise and accumulate at the surface in excess, through evaporation. The soil is dry for such long periods and to such a depth that young replacement plants may not mature, and ultimately even deep-rooted plants may not be able to exist. The resulting lack of vegetation cover allows a high rate of erosion both by wind and rain.

The sub-tropical anticyclones like the trade winds are due to geophysical causes, and so are quite unalterable by human agency. The fitful cloud and rainfall on their borders depends on the degree to which disturbances whether local or from outside can upset the general anticyclonic regime. This degree may vary from time to time but the cores of the great deserts have most probably been relatively arid from far back into geological time and must remain so into the future.

Factors Affecting the Availability of Desert Moisture

The simple measurement or classification of desert conditions in terms of lack of moisture is not possible. Too many factors enter. First one must be careful to distinguish those special areas which do not rely at all on the present day rainfall of the region because they get adequate and reliable water some other way. Second we have

the factors introduced by surface relief, soil and geological structure, which cause great variations from place to place in the amount of available water. Third we have the probability of prolonged periods of cloud associated with the rainfall. Fourth and perhaps most important of all we have the variability of rainfall from one year to another. In some cases fog, frost-rime and dew may also be important.

Exclusion of Permanently Irrigated Areas

Life can luxuriate in the atmospherically driest spots on earth provided adequate and reliable water is made available (and provided this water can also drain away). The words adequate and reliable should here be emphasised. Such permanently irrigated spots have of course many specialised biological interests, but they are clearly not themselves part of a desert, though they may be surrounded by desert. The clearest example is an area to which the supply comes direct by river or canal from elsewhere beyond the desert. Another not so well recognised example is the oasis fed from a large artesian reservoir beneath the desert. Here the supply comes not from elsewhere but from elsewhen – from the fossil water of the rains of long ago. When geological permeability limits the rate of supply and the sites are limited economically by the pumping lift from the water table to the surface, the supply is virtually inexhaustable. Desert biology ought therefore to be confined to life that relies on the precarious atmospheric moisture supplied from within the desert region itself.

Variations in Available Water Supplies from Place to Place

Effect of surface relief, soil and geology.

Because of the high evaporation light showers and dew ought to be excluded from any estimate of the effective mean annual rainfall, except for those forms of life which are specially adapted to absorb and store moisture very quickly. To what extent this is possible appears to need a good deal more investigation.

Owing to surface dryness, lack of plant cover and to the fact that desert rainfall in general is characterised by heavy and infrequent storms, run-off is high and local sub-surface storage low. Hence we may get very strong contrasts in the available moisture between the catchment grounds and the drainage lines which thread them. If the geology is suitable we may get considerable storage in shallow underground pools along the drainage lines, where water is preserved from evaporation and is near enough to the surface to be directly available. In this case one finds narrow streaks of vegetation threading barren country. In other cases the run-off water flows too deep below the drainage lines, or there are no impermeable rock barriers to hold it up. On the other hand desert rainfall is markedly affected by changes in ground elevation. An isolated group of hills a few hundred metres high may attract rainfall many times that over the surrounding country. So if the drainage lines are highly permeable to some depth, we may find life confined to the high ground and none below.

It is these places, where a good water supply is concentrated along the drainage lines, but where not much is now directly available, that offer the greatest scope for artificial improvement. Mislead by unfounded theories of very recent climatic change,

we are only just realising how much was achieved on these lines in ancient times with no more rain than now falls and later destroyed. This is a matter for engineers and geologists.

Wind Erosion Deserts. Sand Surfaces

As one approaches the cores of the great desert regions and rainfall becomes less and less frequent, a stage is reached at which erosion by wind has for ages exceeded that by water. The landscape becomes lunar. Stony plateaux alternate with escarpments, isolated hills, gentle isolated depressions and wide sand-covered plains. Drainage lines fade out and disappear. Since concentration of run-off may be negligible, variation in the available moisture from place to place now depends on local increases in elevation which attract more frequent rain, and on the capacity of the general surface soil to absorb and retain rain where it falls.

When the soil is suitable in this respect temporary grazing springing up from dormant seeds is able to mature and seed itself from a single rain storm after several years of drought. A limit is probably set to the period by the viability of the seed and its physical durability under conditions of sand blast and strong solar radiation. The best soil is undoubtedly blown sand which is relatively clean of fine dust particles between the grains. Water can descend very quickly through this soil since its anti-wetting property is low and its permeability high. Owing to capillary tension a given charge of water applied at the surface of dry sand will sink to a certain depth and no more, the depth being something of the order of eight times the immediate precipitation. Water which has reached a depth of 20 to 30 cm. remains as a moist unsaturated zone for several years because, sand being a very poor conductor of heat, the temperature is constant and 'breathing' nil. The sand both above and below is dry. A sand accumulation is a good desert soil for two other reasons. In a wind erosion plain it is the only place where deposition can balance removal; and it produces the only sloping surfaces capable of appreciable local run-off concentration. Hence one finds that the most favourable vegetation sites, indeed the only sites, lie along the lower gentle slopes of dunes.

I suggest that since blown sand has an almost constant composition and texture it might well be used as a standard soil for the purpose of estimating from the presence or absence of vegetation the mean useful rainfall of those areas for which no long-period records are available.

Variability of Rainfall from Year to Year. Unreliability of Records

In temperate climates where adequate rain falls throughout the year we are accustomed to some deficit in any year from the mean annual value, and we do not bother about it. But as the mean annual value decreases towards a desert region, and becomes confined to one season only, the expected deficit does not obligingly diminish in proportion. A stage is reached at which the probable deficit at any one place is of the same order as the mean annual rainfall. Beyond this stage the probable rainless period exceeds one year. Instead of asking 'have the rains been good this year?' we

begin to ask 'has it rained this year?' or even 'how many years ago did you have rain here?'.

I have noticed a tendency for Western civilisation to limit consideration of deserts to areas where some though inadequate rain falls every year, and to neglect the rest. This is convenient for those who try to measure the degree of aridity in terms of mean annual rainfall, but it leaves the general picture of desert biology, and even of human desert ecology, very incomplete. I think we have been mislead by rainfall maps. Lack of data forces them to lump all desert regions into one final omnibus category of say 250 m/m to zero mean annual rainfall. Whereas if we had enough data to spread this category on a logarithmic scale we should see biology stretching out far beyond the limit of annual rain.

For the more arid areas rainfall data is both inadequate and unreliable, and must remain so until we have 10-year automatic recorders. For it is against human nature to look conscientiously at an empty rain gauge for several years on end. By the time rain does come the gauge has probably been put to some other use, or the observer is elsewhere. It is the rule in some more rain-favoured countries for the gauges to be stored during the dry season and put out on a fixed date, and it is not unknown for a single widespread rain storm exceeding a whole year's mean to remain unrecorded, because it fell too soon. Moreover desert recording stations coincide with human habitation which needs permanent water, i.e. with spots of least elevation. Hence their recorded rainfall is probably considerably lower than elsewhere around.

Beyond the limit of annual rains the biological significance of mean precipitation dwindles rapidly. I suggest that the dominant factor which takes its place is the mean period between effective storms. I would define an effective storm as a fall of such magnitude that some water remains availably stored in favoured spots such as sand, mud pans and rock fissures after immediate surface evaporation has ceased.

The mean rainless period, in years, unlike the mean annual rainfall which needs careful quantitative measurement under very adverse conditions, already exists as a clear estimate in the minds of nomads. Their lives depend on it. And this estimate could be extracted by careful questioning. A fair estimate of the quantity of rain from an effective storm could also be made from descriptions of the degree of flooding.

It is just possible that the mean rainless period, which we could get, might be linked approximately with the mean annual rainfall, which we cannot get, and the latter, though insignificant, as thus obtained indirectly, could then still be used for the sake of continuity of the measuring scale. Various scrappy bits of information rather suggest that the precipitation from a mean effective storm remains fairly constant from one part of a given desert region to another, provided due allowance is made for the effect of ground elevation. For N.E. Africa which includes the most arid areas in the world I would put this constant at 15 to 20 m/m. Allowing 50% run-off concentration this figure agrees with the precipitation needed to soak sand to a depth of 20 to 30 cm. Similarly a guess can be made of the proportion which effective rain bears to the total rain. We might put this at ⅓ and assume that ⅔ of the total rain falls as light showers and can be neglected.

On these rough assumptions, if R is the mean annual rain as measured by a gauge, E is the effective mean, and T is the mean number of years or fractions of a year between effective storms, we have $E = c/T$, and $R = 3E = 3c/T$, where c is the effective storm constant which I will take as 18 m/m for the Libyan Desert. For the neighbourhood of Cairo, where $R = 40$ m/m, we get $T = 1.5$ years, and we should therefore expect patches of blown sand, away from the concentration in wadis, to become green most but not every year, which is about right. The assumed constant for an effective storm and the ratio of effective to total rain are of course very tentative, and need investigation. But the general idea may prove useful in default of any other means of estimating infrequent rain. There are I believe no permanently inhabited places in the world where an effective storm has not occurred in living memory. And the experience of travellers in the remote interior of the Libyan Desert suggests that this applies even here too. Odd bits of local information from this desert seem to indicate a general figure for T between 30 and 50 years, reduced to 4 to 10 years for the few isolated bits of high ground. Taking therefore a general figure of 35 years for T for the Libyan Desert as a whole, we get a mean effective annual rainfall at the present day of half a millimetre and a quite unmeasurable gauge figure of perhaps three times this.

Nomadic Life

Rain over a great desert region does not fall everywhere at the same time, or in the same year. Nomadism depends on this fact. It enables a whole tribe to live permanently in an area where effective rain falls at any one place only once in two or more years. An extreme case is that of the indigenous Libyan Desert Tibu who till recently wandered in small groups across hundreds of kilometres of lifeless 30-50 year country from one favoured hill spot of 4 to 10 year rain to another, with a few sheep or goats and even with a cow. Wild nomad fauna such as addax antelope seem to roam over the same rainfall range. We also have the semi-nomad, based on the desert fringe, who in certain years migrates desertwards with his cattle, but without water, for the grazing to be had off 3 to 5 year areas, and himself drinks nothing but his cattle's milk for six months or more.

Civilisation seems to have overlooked the nomad way of life, even though it exports meat. Surely no other way could be persuaded to produce anything at all from large areas of the world. But for some reason one never hears it suggested that nomadism might be encouraged and may-be modernised. Better varieties of the specialised herbage might be introduced gradually, better control of grazing, radio for the more rapid spread of news of rain elsewhere. Why not, if we wish seriously to improve the productivity of deserts? As things are, nomadism tends to be discouraged as a political nuisance. If traditional nomadism is allowed to die, as it is rapidly doing, for example where oil-fields are being developed, the chances of re-creating this way of life seem remote. Vast areas which can now produce and export at least some food will then be permanently unproductive.

Effect of Small Long-Period Rainfall Changes

In extreme cases of aridity where the remembered rainless period approaches the span of human life it is of course impossible to get at the real mean period. This

would need many centuries of records. Indeed on this time scale the mean rain regime may never be constant. And a small climatic change would have a very marked biological effect. Using the rough rainfall scale I have mentioned earlier, an increase of 8 m/m only in the mean effective annual rainfall (say 24 m/m by gauge) would make nomad life possible over most of the now lifeless core of the Libyan Desert. Thirty to fifty year country would get an effective storm every other year. This must roughly have been the condition in Neolithic times, may-be until as recently as 2000 BC, over the southern half or more of what is now dead land. Significantly one finds their camp sites concentrated towards the sands.

Effect of Cloud and the Season of Rain. Effect of Wind Direction

Excluding the monsoon deserts of Asia it is a general rule that the tropical fringe of a dry desert gets summer rain whereas the temperate fringe gets its rain in winter. But in spite of the higher temperature it seems easier for a general herb cover to revive under conditions of infrequent summer than of winter rains. The likely explanation lies in the more continuous cloudy period associated with the season of summer rain. On the harsher temperate fringe the growth of occasional spring vegetation depends markedly on the duration of the less frequent cloud periods after rain.

There is a general tendency too for the winds of dry deserts to blow across them towards the tropics. This may affect the methods adopted by specialised plants to maintain themselves within their desert habitat by seed transportation. Where the wind is very uni-directional as in the Libyan Desert one notices that on the fringe nearest the temperate zone the desertward wind is made use of and plants of the 'tumbleweed' type abound, whereas on the tropical leeward fringe the seeds or even whole transportable plants tend to be barbed, to enable nomad fauna to carry them against the wind.

A more important wind effect is the carriage of loess-forming dust from the wind-eroded desert core outwards to and far beyond the fringe. The quantity so transported must be enormous. Good evidence exists(1) of a desert surface being lowered 23 metres since mid-palaeolithic times – say 4 cm. per century. It is interesting to speculate on how much less fertile the surrounding lands would be without the benefit of the desert.

The Biological Limit

In most desert regions the biological limit is never reached. In the Libyan Desert trees may live on purely local catchment in places specially favoured by shade and underground storage where it is said to rain only once in 15 years, (mean effective annual rainfall about 1 m/m perhaps). Jerboa have been found where no other local life is apparent, but they seem limited to within say 50 km. downwind of seeding plants. Maybe they get their moisture from dew. The most extreme ecology I know of is that of the few hawks and snakes who live in utterly lifeless country where there is no locally produced nourishment at all. Their ecology must be based wholly on casualties from trans-desert bird migrations. But this in a way is cheating.

(1) G.W.Murray, 1951, *Geogr. J.*, **117** (4), 422-434.

THE AVAILABILITY OF UNDERGROUND WATER IN HOT DESERTS

Professor F.W.Shotton.

(*Birmingham*)

This paper claims to be nothing more than a general survey of the problems and possibilities of obtaining water from underground in the really dry and hot parts of the earth's surface where, without it, human existence would be impossible. If its conclusions are rather pessimistic, their recording may nevertheless be desirable as a counter to the optimism which is often expressed, usually in broad generalisations, and which so frequently proves to be based on experience in semi-deserts where rainfall is by no means unimportant.

In full desert, vegetation is either non-existent or scanty and specialised. Often such plants that exist spring into a short-lived period of abundance after the rare event of rain following perhaps years of quiescence. It is obvious that to convert such regions into productive areas on any useful scale, a regular supply of water must be ensured. This is true even if special drought resistant crops are developed, for these can only be expected to grow when they are being supplied with water. It is not my intention to discuss here those cases such as the valleys of the Nile and the Euphrates or that peculiar accident, the Fayum depression, which though truly desert in climate, can draw irrigation water from large rivers. Situations of this sort are usually fully developed and, even where this is not the case, the controlling factors of topography and volume of the river's flow can clearly be assessed. Over most desert areas, no gift of a large river is there for the taking, and any hope of increased productivity – of productivity at all – lies in the development of underground water.

Water obtained by means of wells and pumps must, apart from any question of economics, satisfy two conditions:-

(a) It must be produced in sufficient quantity and

(b) It must have a quality, judged by its dissolved constituents, acceptable to man for his own drinking, for watering his stock, and for the irrigation of his crops.

The second factor may be discussed first. Much information on this point has been summarized by Dixey[1] and it is quite clear that the limits of quality for different purposes may be broadly lain down, even if there is no general agreement on exact figures for these limits.

The salts which are commonly found in important amounts in water are common salt (sodium chloride), the carbonates and bicarbonates of calcium, magnesium and sodium and the sulphates of the same elements. Not all can occur together, for some are incompatible; and the carbonates and bicarbonates of calcium and magnesium, and calcium sulphate, though important in producing 'hardness', are of such low solubility that they do not in themselves affect the limits of potability. Sodium chloride is often the dominant constituent and may conveniently be taken as the basis for assessing the quality of a desert water – remembering always that the sulphates of sodium and mag-

(1) Dixey, F. 1950, *A Practical Handbook of Water Supply,* 2nd Ed., London : Murby.

nesium, with their purgative properties, cannot be present in quantity without seriously affecting the direct use of the water by man and his domestic animals and that 'black alkali' (sodium carbonate and bicarbonate), even in small amounts, is not acceptable to plants at present grown as crops.

Ideas on the standard of water acceptable to man for drinking have change considerably in recent years. We may now take as a fact that water with a salinity of 3000 parts by weight of NaCl per million of water can be drunk regularly by human beings in a desert climate, that a figure of 4000 unaccompanied by important quantities of other salts is acceptable, and that for short periods even a figure of 5000 is endurable. Domestic animals are even more tolerant of dissolved constituents than man though there is no close agreement on the worst limits of quality. Thus to take three examples from Australia, we find Jewell[1] in Victoria, stating that 3000 parts of *total* dissolved salts (not simply sodium chloride) per million is safe for working horses, dairy cattle and pigs, and setting a normal limit of 7000 and an emergency one of 10,000 for grazing cattle and sheep. Jack[2], in South Australia states that horses will thrive on water with 1 ounce of sodium chloride per gallon (6260 parts per million) and sets the upper limits for living as 7800 for horses, 9400 for cattle and 15,600 for sheep – unless magnesium sulphate is present, when the figures must be lowered. Edgeworth David and Browne[3] giving figures expressed as total solids, set limits even beyond those of Jack's – 8000 for horses in work, 13,500 for horses at grass, 14,000 for cattle and 19,000 for sheep. However we attempt to reconcile these somewhat discrepant figures, it is apparent that man is rather less tolerant than are his herds, but that both can drink water which, as will be seen later, is of a quality not infrequently obtainable in deserts.

To obtain water of a quality suitable for crop-irrigation is a far more difficult matter. There are certain salts – the alkali carbonates and bicarbonates (black alkali) – which are only acceptable to plants in very small concentration. Figures of between 100 and 200 parts per million have been given as limits and such amounts are often exceeded in desert waters considered to be of good drinking quality. Apart from these special constituents, the total amount of dissolved solids in irrigation water must also be much below the limits of drinking water. It is not that many plants are intolerant of brackish water. I have myself seen date palms and tamarisk growing well in ground water with 6000 parts of NaCl per million – a water which a man could not take; but the process of irrigation in a desert climate is inevitably accompanied by evaporation, with the gradual concentration of salts in the soil to a point where plant growth is inhibited. The practical limit that has been given for the total solids in irrigation water is only 700 per million. No doubt some easing of the stringency of this figure is permissible in semi-deserts, where there is sufficient rainfall to leach out some of the accumulating salts, but in this paper I am concerned primarily with true deserts. In these, the high quality necessary for irrigation water is the controlling factor on pro-

(1) Jewell, N.R., 1927, Water for Stock. *J. Agric. Victoria.*
(2) Jack, R.L., 1914, *Bull. Geol. Surv. S. Australia*, No. 3.
(3) Edgeworth David, Sir T.W. & Browne, W.R., 1950. *The Geology of the Commonwealth of Australia*, 2, 514-593.

ductivity. Unless man finds such water in quantity, he can neither grow regular crops for their own sake nor as fodder for his herds. The truth of this is exemplified in the Australian artesian basins, where very few of the thousands of boreholes are used for irrigation schemes, because of the amount of dissolved salts. Consequently most of the boreholes lie in the semi-desert, where rainfall, exceeding 10 inches a year, provides natural grazing. If long continued drought causes this to fail, water from boreholes may prevent the cattle dying of thirst but not of starvation.

If, therefore, the desert is to blossom, water of irrigation quality and quantity has to be found. Underground water is dependent on rainfall, for we can discount juvenile water in this connection. Probably no desert is completely rainless, but a low percolation is accompanied by a paucity or absence of springs and that, it its turn, means a slow underground movement of water with ample opportunity to dissolve salts from the containing rocks. Along the Palestine coastal plain, which is not a true desert, we can see this relationship between declining rainfall and increase in the mineralisation of the water until at Rafah, on the Sinai frontier, it is not easy to obtain even satisfactory drinking water. Before reaching this point we can see the increasing difficulty of running satisfactory irrigation schemes. My experience of North Egypt and Libya during the war convinced me that a water table could be found almost everywhere in this desert but usually of such high salinity that a random well has small chance of finding drinkable water and next to no chance of water of irrigation quality.

Although this taking up of salts in solution is controlled also by the characters of the rock holding the water, I think it is a fair assumption that irrigation quality water is not to be expected in a desert from its own local and limited rainfall unless exceptional conditions exist. Of a number of such conditions, two may be mentioned. The first occurs when newly-percolated rain, making its way to the water table, finds difficulty in mixing with the general body of saline water. In the Western Desert during the war many water points were established through this cause(1), with salinities from 200 to 2000 parts per million in a vast area where normally the salinity stood at 5000 or 6000 (i.e. unpotable) and exceptionally went up to 60,000. Characteristic of such wells were the thin depth of good water (typically only a few feet), the very sporadic distribution of these patches (undrinkable water could exist only 100 yards away), the gradual tendency to become more saline with pumping and the small yield which rarely exceeded a few hundred gallons an hour. Indeed, the smallness of yield is an inevitable corollary of the fresh water – a fissure or pore system open enough to give a large yield would not permit the fresh water to remain unmixed with the salt in the first place. Such wells, therefore, have no importance in irrigation prospects.

The second possibility to be discussed is that of perched water, where geological structure causes the holding up of water above and quite separate from the main table. The controlling factor is often a bed of shale or clay occurring as a lens or a fold between two aquifers. Such a structure has its limits and as rain joins it, there must be an overflow from the perched position either as a spring (which is unusual in deserts) or underground to the main water table. In this way, a one-way movement may be set

(1) Shotton, F.W., 1946, *Wat. & Wat. Engng.* **49**, 218-226.

up, leaching out the soluble salts from the upper containing rock until the water therein has little dissolved matter to take up.

Several examples of this type were developed in the Western Desert during the war, the most notable being at Fuka[1]. Its structure, with a bed of clay separating two limestones and folded into an elongate basin, has been fully described. From measurements of exhaustion and replenishment after rain, it was calculated that 25,000 gallons a day could be taken out without risk of failure and that the structure carried a reserve equal to five years' supply to tide over any winters of low rain replenishment. Hence there would appear here to be the possibility of a small irrigation scheme (but only of about 20 acres, if we are to accept David's figures and allow also for use of the winter rains) provided that the water was good enough. Actually the average of several analyses shows:

Total solids	1400 parts per million
Sodium chloride	750 " " "
Sodium carbonate	50 " " "
Sodium sulphate	160 " " "
Calcium (plus magnesium) carbonate	330 " " "

It is thus somewhat above the limit mentioned earlier, but in view of the fact that there is here a winter rainfall of perhaps 6 inches which would tend to dissolve out such salts as had been deposited in the soil during the preceding summer, an irrigation scheme appears possible.

What must be emphasized, however, is the pitiful inadequacy of this, our only spectacular example of perched water – a structure of 170 acres, capable of irrigating 20 acres, in a desert that was considerably if not exhaustively probed over perhaps 8000 square miles.

Wartime experience in the eastern Egyptian desert (Red Sea Hills), where rainfall is extremely small and sporadic, showed that by careful attention to geology, aided by geophysical measurements, underground reservoirs of drinkable water could be found[2]. Of 10 wells with drinkable water, 5 were of irrigation quality; but the yields were only of a few hundred gallons an hour with a limited life, and so useless for irrigation schemes.

I feel therefore, that it should be emphasised that in hot deserts, with their very low rainfall, the derivation from this of underground supplies large enough and fresh enough for irrigation must be an exceptional occurrence, the result of a combination of geological accidents that can only occur very rarely.

There remains one other source of hope. Some deserts may have a geological structure where a sedimentary formation, occurring at depth, eventually outcrops in an area of normal rainfall beyond the confines of the desert. Provided this formation is water-conducting and insulated from contamination with whatever higher saline water exists, it may be entered by borings and good water may be obtained. Notable examples

(1) Shotton, F.W., 1944, The Fuka Basin. *Roy. Engrs. J.*, 107-9, 1946. *Wat. & Wat. Engng* **49**, 257-263.

(2) Paver, A.L., 1946, *Wat. & Wat. Engng.* **49**, 653-662.

of this effect are provided by the deep artesian wells of Tunis and Tripolitania, by the Nubian Sandstone (Cretaceous) which outcrops in the Sudan but gives good water to the depressions of Kharga and Dakhla, 650 miles to the north and, of course, by the various artesian basins of Australia.

It is undoubtedly in such large-scale geological structures that the main hopes for irrigating deserts lie. It would be well not to exaggerate those hopes. Artesian supplies in a desert can only materialise in large and useful amounts (a) if the aquifer outcrops outside the desert region, i.e. in an area of adequate rainfall; (b) if the aquifer has high permeability beneath the desert, so that there can be underground transfer of water and the obtaining of high yields; (c) if the quality of the water remains suitable for use in its long underground journey from the intake; (d) if the water budget is balanced – i.e. the extraction is balanced by intake.

Mainly on the second ground, Du Toit held out little hope of artesian supplies from the Karroo. In the Great Artesian Basin of Australia, much of the water is mineralised as a result of its underground journey from intake to well, to the extent that although it is acceptable to cattle and to man, it is not usable for irrigation.

The great African hollows of Kharga and Dahkla, where artesian springs were once abundant, are notable examples of large-scale irrigation (mainly of date groves) from artesian water of good quality in an area which is virtually rainless; but attempts to intensify that cultivation have been accompanied by a continuous demand for more and deeper boreholes, with a steady lowering of water pressure and the drying up of springs. The artesian water,here, then, is a slowly wasting asset on the present scale of cultivation. Such a picture does not encourage any belief in a spectacular increase in the use of the Nubian Sandstone water in the Western Desert, even if low-lying areas can be found where the water may be met at depths sufficiently shallow to allow economic pumping. Nor is there much hope that this good quality water extends as far north as the Egyptian and Libyan coast, in view of the bad water of the northern oases of Siwa and Jiarabub and the saline water in a deep bore at Tobruk.

The deserts mentioned above are more fortunate than others which seem to have no hope of a deep-seated supply. The great Arabian Desert, for instance, probably has no suitable geological structure for artesian supply and even if it had, it could not satisfy the necessary condition of an outcrop in a region of good rainfall beyond the confines of the desert.

This paper is a very general survey, biassed perhaps by the deserts which I know personally. It will have fulfilled its purpose if it sounds a warning against the optimism which sometimes pervades discussions on the conversion of deserts to useful productive land. Again it must be emphasised, however, that only full desert has been under discussion. In those fringe areas (South Palestine and parts of Jordan are good examples) where nature has provided at some period of the year an adequate rainfall and yet turns the country to arid desert in the summer, there is every incentive to search for underground water and to use it to balance out the irregularities of the rainfall. The search may often be long and difficult and the results must always conform to the law that more water cannot be taken from the ground than soaks into it; but subject to those limitations, there is a future for parts of the semi-desert earth which most of the true desert cannot hope to share.

SOME BIOCLIMATIC OBSERVATIONS IN THE EGYPTIAN DESERT

Dr C.B. Williams.

(*Rothamsted Experimental Station*)

I resided in Egypt from July 1921 to June 1927, and during this period I made three short expeditions to the hilly desert to the south-east of Cairo to take observations on bioclimatic – or what perhaps today would be called microclimatic conditions. The object was to discover the range of temperature and other environment conditions available to animals with a power of choice, and of movement over short distances.

The results have already been published in technical and scientific bulletins of the Ministry of Agriculture of Egypt (see bibliography at end), but as these are not easy to consult in libraries, it was thought that a new summary might be useful to ecologists.

The locality chosen was in Wady Digla, a dried watercourse about twelve miles south-east of Cairo and about seven miles from the nearest cultivation in the Nile Valley. The wady (or valley) at the point chosen runs from east to west and is about 300 yards across at the top, about 80 yards across at the bottom and about 200 feet deep. The rock is a pale brown limestone. Rain falls on an average not more than once a year.

Three visits of eight days each were made in August 1922, March 1923 and December 1923, and on each occasion meteorological readings were taken, for seven consecutive days, every hour from 5 a.m. to 11 p.m. and again at 1 a.m. In addition to these three longer visits, many one or two day visits were made at all times of the year, and on some of these temperature and humidity conditions were recorded.

Readings were taken in a variety of locations, including a Stevenson's screen in the middle of the wady – in the shade of the rock on the south side of the wady – under a large rock where it was just possible to crawl – on the plateau above the wady – at different depths up to 30 cms. in a sand patch alongside the dried water course – at a depth of about 75 cms. down a Jerboa burrow – in a bird's nest in a bush, and in another hole in a rock - in two 'ant-lion' pits one in the sun and one in the shade – and at various depths in two caves. The records included black and white bulb temperatures – wet and dry bulb temperatures with a sling-psychrometer – wind with two cup anemometers – and evaporation with 'Piche' evaporometers.

Table I shows a summary of most temperature and humidity records (except those in the caves) in each of the three periods of observation, and Fig. 1 shows diagramatically the means and extremes in many of the habitats.

It will be seen that in August the black bulb thermometer reached 74°C (166°F), the surface sand reached 58°C (136°F) and the temperature in a bush reached 44°C (111°F), while the shade temperatures only reached 35°C (95°F) which was less than the maximum of the sand at 20 cms. The August week was not exceptionally hot, and shade temperatures 5° or even 10°C higher might well occur at this time of the year. During this period a temperature of 44.2°C (112°F) was recorded in the sand of an 'ant-lion' pit, and at this temperature the ant-lion larva just below the surface immediately captured an insect which was dropped into the pit.

TABLE I

TEMPERATURES °C	August 1922	March 1923	Dec. 1923
IN SCREEN			
Abs. Max.	–	23.8	22.1
Mean Max.	–	22.2	20.7
Mean Min.	–	10.0	10.2
Abs. Min.	–	7.2	8.0
Mean Range	–	12.3	10.4
SHADY SIDE OF WADY			
Abs. Max	35.9	22.3	21.6
Mean Max.	34.5	20.7	20.2
Mean Min.	22.5	10.4	11.4
Abs. Min.	21.2	7.8	10.0
Mean Range	12.0	10.4	8.7
BLACK BULB			
Abs. Max.	74.4	60.8	57.5
Mean Max.	72.4	59.4	56.4
UNDER LARGE ROCK			
Abs. Max.	37.0	21.0	–
Mean Max.	35.2	19.7	–
Mean Min.	24.4	12.5	–
Abs. Min.	23.2	11.0	–
BIRDS NEST IN BUSH			
Abs. Max.	43.3	26.4	–
Mean Max.	42.2	24.6	–
Mean Min.	23.1	10.4	–
Abs. Min.	21.9	7.0	–
BIRDS NEST IN ROCK			
Abs. Max.	–	19.5	18.0
Mean Max.	–	18.3	16.9
Mean Min.	–	13.7	13.6
Abs. Min.	–	12.5	12.0
GROUND MINIMUM			
Mean Min.	–	8.1	7.7
Abs. Min.	–	6.2	5.0

SAND IN WADY	August 1922	March 1923	Dec. 1923
SURFACE			
Abs. Max.	58.2	43.6	29.3
Mean Max.	56.1	39.2	28.5
Mean Min.	20.6	7.6	8.4
Abs. Min.	17.5	5.7	6.6
Mean Range	36.0	31.7	20.2
AT 10 CMS.			
Abs. Max.	41.3	26.4	21.0
Mean Max.	40.0	25.6	20.0
Mean Min.	27.6	15.1	12.9
Abs. Min.	24.4	13.9	12.0
Mean Range	12.9	19.5	7.0
AT 20 CMS.			
Abs. Max.	37.8*	21.7	19.7
Mean Max.	36.0*	21.5	18.6
Mean Min.	30.3*	17.9	16.5
Abs. Min.	29.3*	17.6	16.0
Mean Range	6.4*	3.6	2.1
RELATIVE HUMIDITY %			
Abs. Max.	96	82	97
Mean Max.	82	75	83
Mean Min.	21	29	43
Abs. Min.	16	21	27
Mean Range	61	46	40
VAPOUR PRESSURE (mm.)			
Abs. Max.	20.8	8.6	11.6
Mean Max.	–	7.7	9.7
Mean Min.	–	5.1	7.0
Abs. Min.	5.7	3.9	4.9

* at 18 cms.

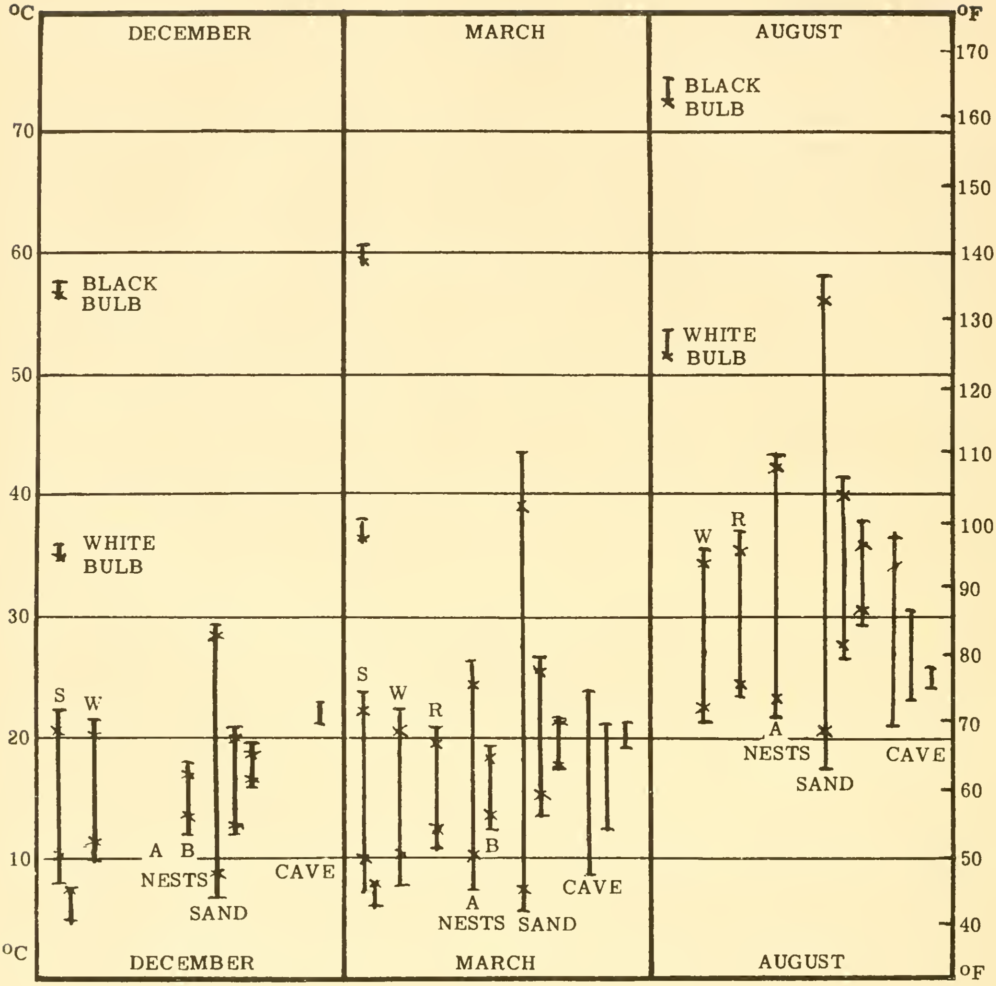

Figure 1.

Wadi Digla near Cairo. Temperature Conditions in Desert.
S = Screen W = Shade in Wadi R = Under Rock. Nests, A = Bush B = in Hole in Rock
Sand at 1. 10. and 20 cms. Cave at Mouth, 5 and 12 metres in.

Fig. 2 shows the hour by hour changes in temperature in some of these locations during five days in August. Apart from the great daily range of temperature in the places exposed to the sun, there should be noted the low range but high average temperature in the Jerboa burrow, and the low range and low average temperature in the sand in the shade, as shown by the ant-lion pit. It is also interesting to note that the maximum temperature at the end of the Jerboa burrow (which was estimated to be about 23 cms. below the surface) occurred about 9-10 p.m. and the minimum about 8-9 a.m., the former about 8 hours and the latter about 4 hours later than the corresponding stage at the surface.

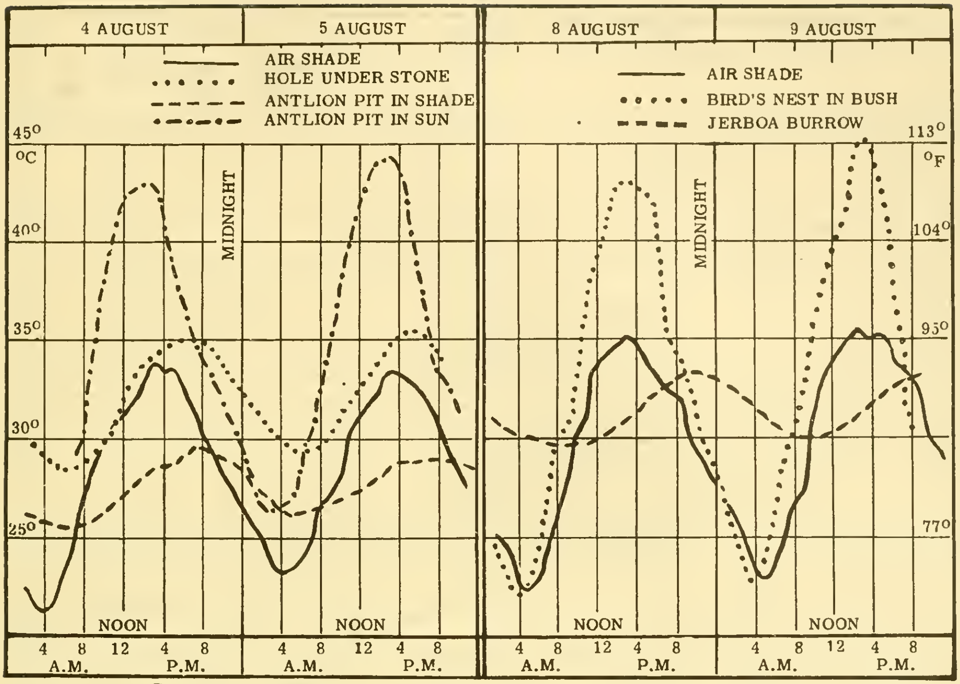

Figure 2.
Hour by Hour Changes in Temperature

Fig. 3 shows the range of combined temperatures and relative humidities covere by hourly observations in the shade on the south side of the wady, calculated from sling-psychrometer readings. In August air temperatures ranged from 21° to nearly 37°C and relative humidity from 95% in the early morning to 17% in the late afternoon. The range of humidity was slightly less (with distinctly lower temperatures) in March, but reached almost to saturation in December. In this latter week there was, however, a sudden change of air moisture resulting in an unusual range of combined temperature and humidity.

For comparison with the extreme desert conditions in August there is shown the range covered by 24 hourly records taken at sea in the Mediterranean one day in August. The contrast speaks for itself.

As some insects and other animals are known to be active in the low light intensity both at dusk and at dawn, the dusk and dawn records are shown individually in Fig. 3, indicating the very wide difference between the cool damp morning and the warm dry evening conditions.

As many animals burrow in the sand in deserts by day time, perhaps to escape extreme conditions, special attention was paid to changes in temperature at different depths in the flat topped sandy areas which were found here and there along the dried

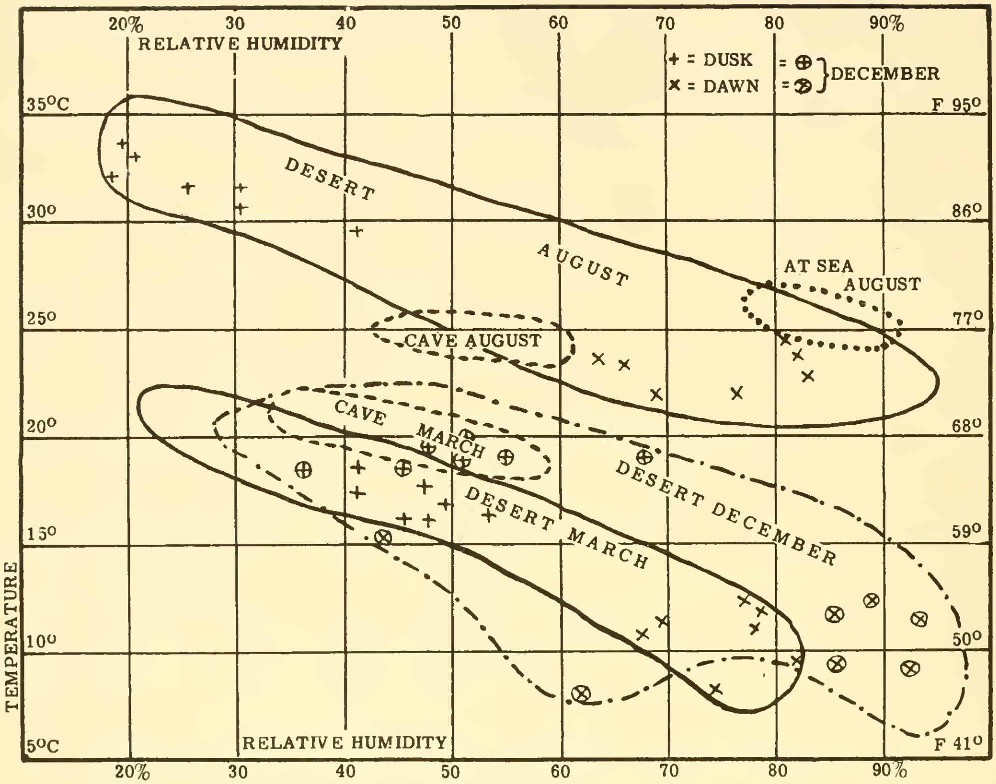

Figure 3.
Combined Temperatures and Relative Humidities

water course in the centre of the wady. Fig. 4 A shows the gradually changing temperature at different levels in the sand during 36 hours in August. Surface temperature reached a maximum of 56°C (133°F) at about 1 p.m.; at 5 cms. the maximum was 44°C (111°F) at about 3 p.m.; at 10 cms. just over 40°C (104°F) at about 5 p.m.; at 18 cms. 36°C (97°F) at about 7 p.m.; while at 28 cms. the temperature only ranged from about 23° to 24°C (73-75°F) with a maximum about midnight. The minima ranged from about 20°C (68°F) at 5 a.m. at the surface to 23°C (73°F) at 28 cms. about mid-day. Fig 4B shows the temperature contours at different depths during the day and Fig. 4C shows the movements of heat in the sand at different times, the surface heating during the day and cooling during the night. The lines where the heat movement is momentarily zero have been called the 'thermostatic lines' (see McKenzie Taylor and Williams 1924).

Fig. 5 shows how the observed changes in temperature at different depths in the sand in August support the theory that the range of temperature at a depth x is given by the formula $R_x = Ra^x$ where R is the range at the surface, and a is a constant for the particular sand or soil. The figure shows above the observed maxima and minima, and below the expected range calculated from the above formula with $a = \cdot 013$, and as 'crosses' the observed ranges which fit extremely closely to the calculated values.

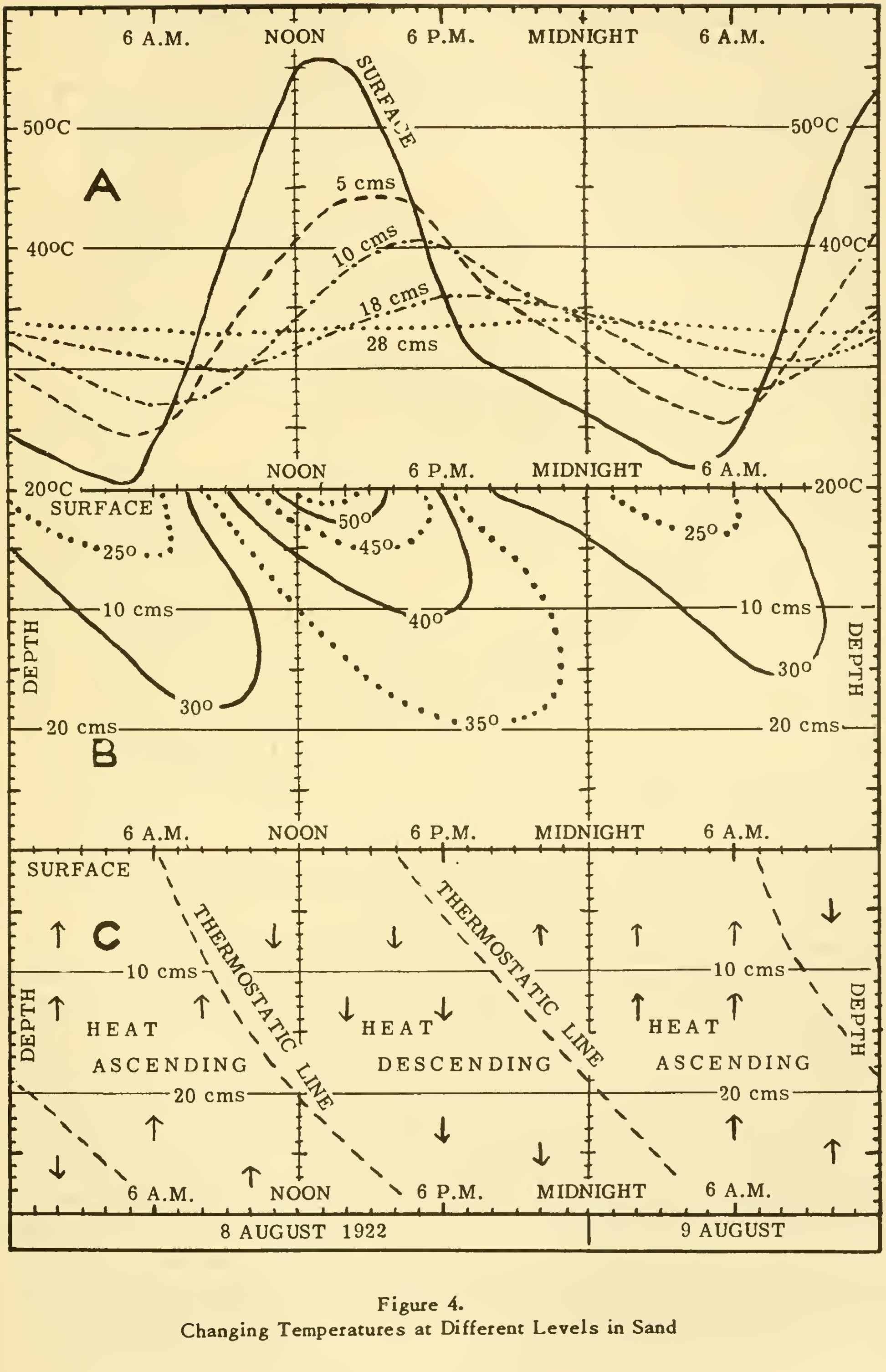

Figure 4.
Changing Temperatures at Different Levels in Sand

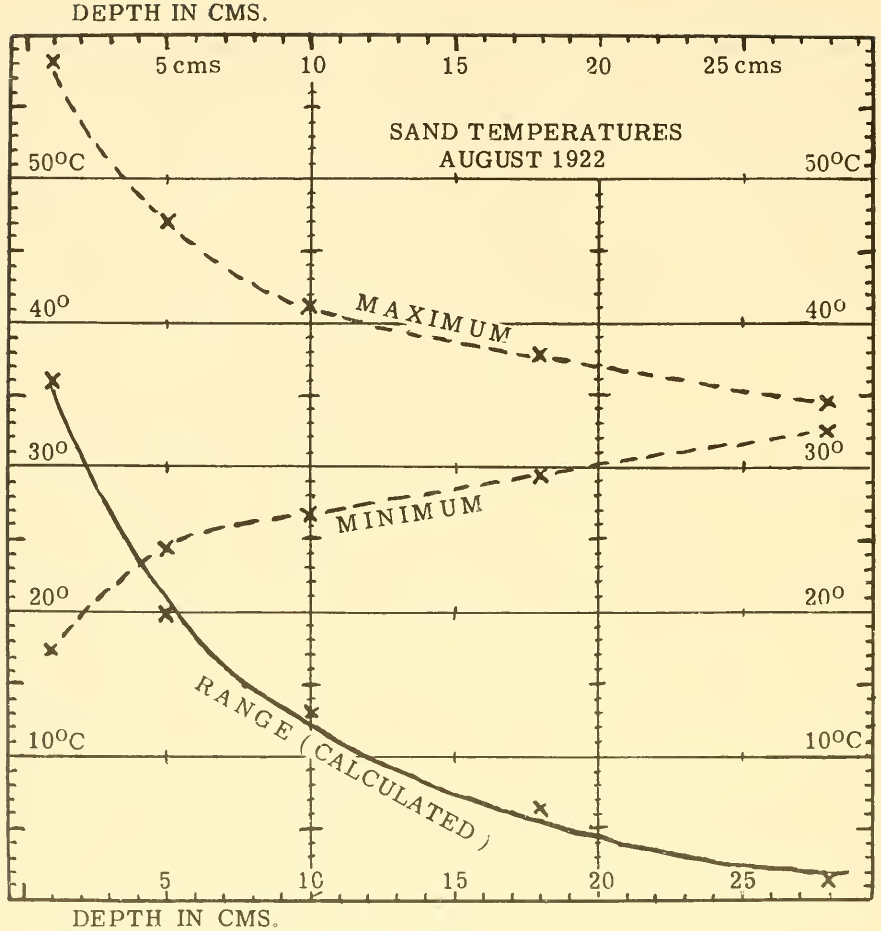

Figure 5.
Temperature in Sand — Observed and Calculated Values

Microclimatic conditions were also investigated in two caves in the sides of the wady, the first cave in August and March, the second in March and December, with a few extra observations at other times of the year. The values for temperature and humidity are shown in Table II, and diagramatically in Fig. 6.

Fig. 6 also illustrates an interesting point with regard to relative humidity. It was found that the vapour pressure inside the cave tends to come into equilibrium with that outside. Vapour pressure is generally lower in winter than in summer, but the difference in temperature results that relative humidity is higher in winter than in summer. Since at a depth of about 20 metres into one of these caves the annual temperature is almost constant it follows that the relative humidity inside the cave tends to be higher in summer than in winter, just the opposite to what is happening outside. It must be remembered, of course, that these caves are surrounded by completely dry rock. Under normal European conditions cave air tends to be quite saturated with moisture.

TABLE II

FIRST CAVE

TEMPERATURE °C	MOUTH	5 METRES	12 METRES
August (min. and max.)	21.0-36.3	23.0-30.4	24.0-25.4
range	15.3	7.4	1.4
March (min. and max.)	8.8-24.0	12.4-21.2	19.3-21.4
range	15.2	8.8	2.1
December (min. and max.)	–	–	21.5-23.0
range	–	–	1.5

SECOND CAVE

TEMPERATURE °C	MOUTH	5 METRES	15 METRES	25 METRES
March	12.0-25.5	19.3-22.3	23.2-23.4	24.2-(25.0)
May	20.0-29.0	22.3-24.3	24.0-24.2	24.0-24.0
September	22.5-33.0	25.4-26.3	24.5-25.0	24.0-24.2
December	10.8-10.8	19.0-23.0	23.2-23.6	23.7-24.0
Total range	22.2°C	7.3°C	1.8°C	1.3°C
RELATIVE HUMIDITY %				
March	28-78	(40)-54	33-35	35-38
May	25-62	37-52	42-47	37-38
September	34-88	50-58	57-60	55-56
December	36-56	33-36	30-39	38-43
Total range	63%	25%	30%	21%
VAPOUR PRESSURE in MM.				
March	6.7- 8.2	(7.9)- 9.0	7.0- 7.3	7.9-(9.1)
May	7.6-10.8	8.3-10.2	9.4-10.3	8.4- 8.6
September	12.9-17.6	12.7-14.1	12.8-14.0	12.3-12.4
December	5.4- 6.9	5.5- 7.5	6.2- 8.6	8.5-(9.5)
Total range	12.2 mm.	8.6 mm.	7.8 mm.	4.5 mm.

During the three periods of observation there was no general deposit of dew on the ground, but one day in August there was dew on the wind gauge, and on twigs of various dried up plants on the plateau above the wady. On this morning the dew point at 5 a.m. was 17°C and the surface soil 17.5°C, so that a very small further fall of temperature would have produced a general ground dew. It is interesting to note in this connection that a desert plant, *Reamuria hirtella* J. and S. of the family Tamaricacea, which was not uncommon in some spots along the wady, was found to be dripping wet in the early morning whenever the relative humidity of the air was above 75%. This was found to be caused by small crystals of sodium chloride on the surface of the plant which absorbed moisture from the atmosphere above this relative humidity.

It will be clear from the above that within a distance of relatively few metres there are available in this type of desert country a very wide range of temperature conditions

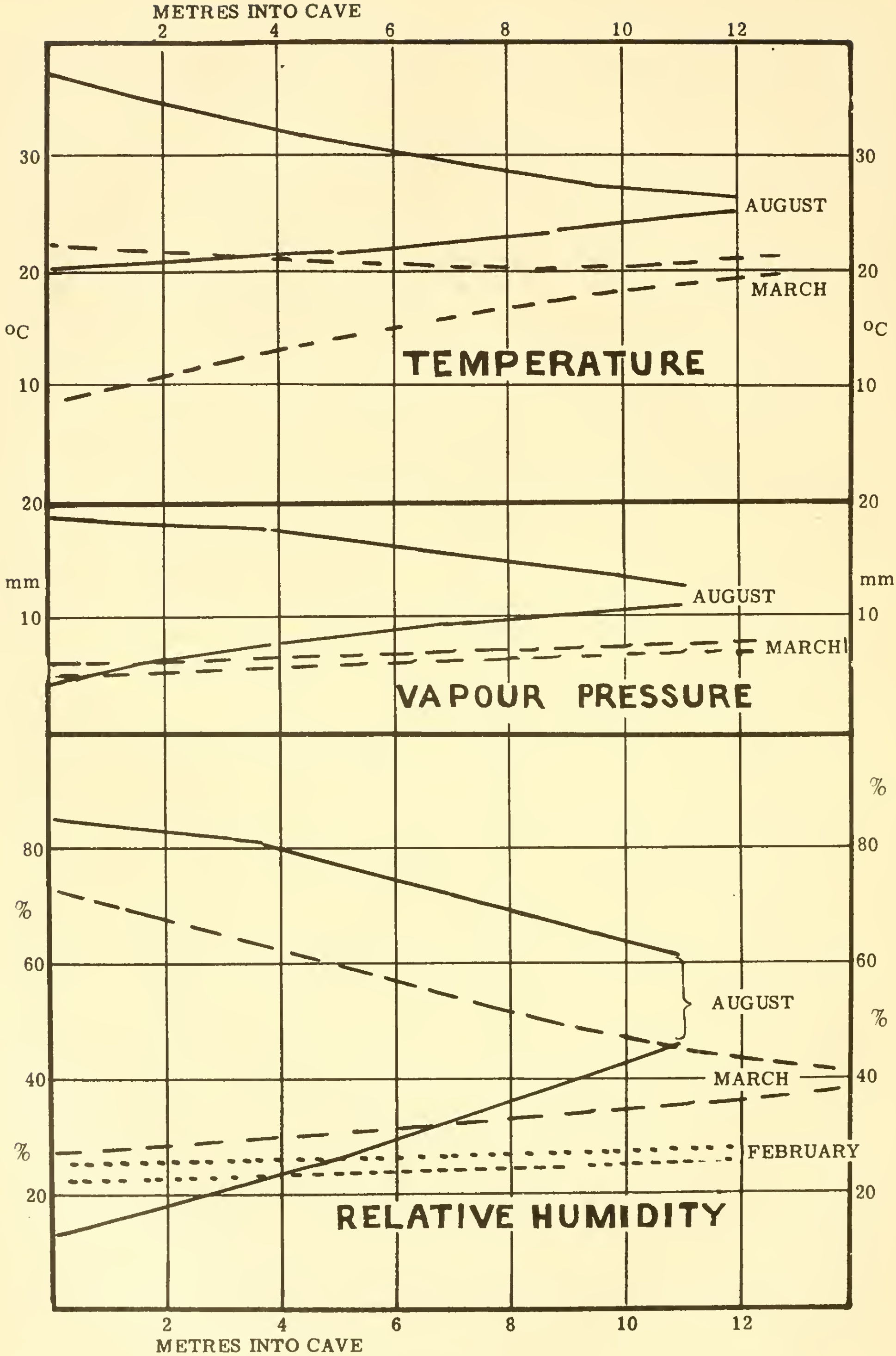

Figure 6.
Temperature and Humidity

from among which an animal can choose by little expenditure of energy. By burrowing deep an animal can avoid the extreme heat of day – and by leaving the burrow at night it can even escape the peak temperature below, as at a foot or so beneath the surface there is a lag of about 12 hours in the time of maximum temperature. Almost as big a choice is available in this hilly type of desert by moving into the more or less permanent shade beneath the steep south side of the valley. An experiment was made one day in August by artificially shading the sand where the temperatures were being measured. The maximum surface temperature under these conditions was 20°C (36°F) lower than the previous day when the sun had been shining, while at 18 cms. deep the maximum (not reached till about 7 p.m.) was 5°C (9°F) lower than the previous day.

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PLANT ECOLOGICAL PROBLEMS IN INCREASING THE PRODUCTIVITY OF ARID AREAS

Dr H. Boyko.*

(*Jerusalem*)

Approximately a third of the surface of the earth (Sears states 31%) is located in arid zones, yet only a relatively small part of this area can be eliminated from this discussion on the basis of being climatically absolute desert. By far the largest parts of the area can be classified as semi-deserts or man-made deserts. If we face the issue of increasing productivity from the point of view of the plant ecologist, we must occupy ourselves primarily with these regions.

Among the tasks of ecology, pasture ecology occupies a position of major importance. I deliberately use the term 'pasture' in order to avoid use of the word 'grasslands', for it is precisely the steppe and prairie regions which constitute the second boundary to the scope of any topic, both objectively and geographically. Though these may also be in an arid region, they are nevertheless always covered by a dense blanket of vegetation, alive or dead, even during the dry season. Between the areas completely under vegetative cover and those of absolute desert which is climatically caused, lies the main area subject to discussion here. Israel provides a very good example. Driving through this small country, we pass within several hours through the majority of the global vegetative zones located in the Northern Hemisphere, namely the forest belt, the steppe belt, the semi-desert belt, and the climatically-caused absolute desert.

From the North-Mediterranean Laurel forest climax we pass through the Eu-Mediterranean, semi-arid *Quercetum cocciferae,* and through the more arid sub-Mediterranean forest association of *Ceratonietum soliquae* into that belt, which occurs globally between the dense forest climax and the steppes, to which the above mentioned association is already a transition stage. This zone I call the arid border forest belt. In south-west Asia it is divided into the Anatolian-Iranian *Quercus Aegilops* belt and the Mauretanian-Iranian *Pistacia mutica* belt. These two intersect in Israel, from whence they strike a wide arc round the Mesopotamian lowlands, the *Pistacia* further inland than the oaks. Adjacent to this border forest belt is the *Stipa* steppe belt, followed by semi-desert and desert. Analogous conditions occur all round the globe in both hemispheres, with the possible exception of Australia. There we find a considerable amount of trees in a climatic zone where elsewhere we would expect only a treeless semi-desert.

This surprising phenomenon may indicate that in Australia tall, woody species have had a much longer geological period in which to adapt themselves to drought resistance than is the case in other continents. In the steppe regions of south-west Asia perennial herbs predominate, after grasses, as in the Anatolian steppe, then the tall feather grasses gain dominance, the cover becomes ever sparser, the bunches are farther apart, and we pass from steppe to semi-desert. Here woody plants, bushes, and bushy perennials predominate, and between them there grow bunches of low grasses of varying density. In the spring, depending on the rainfall of the preceeding weeks,

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there are larger or smaller numbers of annuals, but for a short time only. Areas with less than 100 mm. annual rainfall are to be designated as desert, and only on sand and in the wadis is there somewhat denser vegetation. Under still more arid conditions, only in wadis and oases do we find larger numbers of individuals in what can be called an association.

Such is the natural picture where man has not interfered. This however is seldom the case. The largest part of the border forest belt, has been converted to steppe, the steppes to semi-desert, and semi-deserts into deserts. In the Orient, where overgrazing has been the practice for millenia, and where the equilibrium between plant, animal and man has long been disturbed, this development is especially prominent. In order to create a regeneration here, we must first determine the climax association of the region under consideration.

The reconstruction of the original climax associations, and the mapping thereof, is one of the most important tasks of the plant ecologist in these regions. Without this, planning land-use cannot be on a sound basis. Another line of research is based on the biological rules of climatic extremes. At a boundary of the distribution of a species or of an association, the smallest variations on the environmental conditions are decisive for its existence. Plant ecologists must therefore determine these ecological amplitudes and the geographical boundaries on the one hand, and, learn to recognize the variations in the environment, and to measure them quantitatively on the other. Comparison between the two phenomena will always yield most important and far reaching results.

Furthermore, when we wish to create a more dense plant cover, or to increase the population density of a particular species, we must also take into account shifts in the complex of factors in these boundary regions. I wish to present the example of the 'IE-factor', the factor complex involving insolation and exposure. In the low latitudes, it is surprising what large differences in micro-climate result from variations in the degree of inclination on the same slope. Ashbel found that the difference in insolation between a horizontal surface at the latitude of Jerusalem, and a 40° north facing slope is as great as that between two horizontal surfaces, one located in Jerusalem, and the other in Paris. Testing the results of my own investigations with regard to the decisive effect on vegetation, the same experience has been made in U.S.A., Australia, etc. As a result, we can pass through three distinct floral regions on a northern slope in the Wilderness of Judea east of Jerusalem, all within a few metres of each other. On a 25° slope we find a Mediterranean flora, on horizontal surfaces a Saharo-Sindian, and on intermediate slopes we find a transitional Irano-Turanian flora.

The whole Far Negev, (that is the part of Israel lying south of Beersheba), can be considered to be an especially favourable area for experiments on all arid regions and therefore my department there has set up three permanent observation stations, which are complementary to each other both edaphically and climatically. One is situated in the mountains near the ruins of the ancient city of Abdeh. Here we are attacking problems of pasture regeneration and the utilization under control of the torrential winter floods. The second is at the oasis of Ein Ghadian in Wadi Araba, the deep trench between the Dead Sea and the Red Sea; and the third is the most important Desert Garden at Elath on the Red Sea, where my wife Dr Elizabeth Boyko is in charge.

Our plan for productivization of the mountainous part is, firstly, the regeneration of the severely destroyed climax vegetation in the mountains and on certain sandy plains, which could provide about 4-5 months pasturage a year following regeneration. One may also assume a certain degree of self-sufficiency of the settlers in respect to grain, vegetables, and fruit, if measures are taken to utilize the torrential winter floods in the wadis. The latter problem is more technical, the former is purely geological. In this area, which has been suffering from over-grazing for thousands of years, the theoretical reconstruction of the climax associations depends in the first place on the finding of good fodder plants, especially those rare species in inaccessible places.

Another important task is the determination of the palatibility of the various species, since those of highest palatability are of course most in danger of total extenction. On the other hand, unpalatable plants should also be studied in order to ascertain the reason for their being shunned by grazing animals. Finally, the competitive power of these plants must be evaluated and compared.

It would be helpful if small areas of such destroyed pasture regions that occur in the Orient and in Africa, could be fenced off and protected from grazing for a time. In a very few years important changes indicating the tendency of the natural succession could be observed.

I should like to bring you another example from the Negev. The small shrub *Artemisia herba alba* is scorned by all animals. Consequently it has been able to conquer large areas including all the mountains above the altitude of 450-500 metres. As soon as we eliminate grazing, however, the previously rare tall feather grasses multiply rapidly, indicating a trend towards the actual climax condition, in which good fodder grasses such as *Stipa barbata, Stipa Szowitziana,* certain *Aristida* spp., and others dominate. It is clear that the vigorous fibrous root systems of these bunch grasses can compete with the much weaker roots of *Artemisia herba alba.* The seeds of *Stipa* find good conditions for germination in the bushes of *Artemisia,* and if they are not devoured at an early age, may eliminate the *Artemisia* within a matter of years. Such studies of succession lead to the reconstruction of the climax association, and only on the basis of this can one begin to make serious plans for the conversion of man-made desert and semi-deserts into pasture land.

In the days of the Palestine Mandate I had the opportunity to wander through these remote areas on camel-back and I have therefore been able to observe their development for a number of years. The most striking phenomenon is the increase of good fodder plants after the cessation of grazing. In the Tureibe region, a sandy area of about 30,000 acres, together with my assistant, Mr Tadmor, I carried out an exact statistical study of their development. The unpalatable species remained constant in their population density, while the highly palatable ones have increased in density approximately ten times during the past five years, while there has been no grazing. I am referring principally to *Aristida plumosa, Danthonia forskahlei, Convolvulus lanatus, Argyrolobium uniflorum,* etc. *Calligonum comosum,* a large and valuable fodder bush, has not multiplied during this time. As is the case with many trees and bushes, it apparently needs one or more years of favourable conditions in order to germinate and to multiply naturally. However, multiplication by the means of cuttings is within the range of economic possibility.

We face ecological problems of an entirely different nature when we look for, and even after we have found those desert plants which come under consideration as possible sources of human food or of raw materials. Searching for, and finding them is only the first part of the problem. Their introduction into commerical production is another complicated problem. There are two ways in which the finding of such plants can take place. One is the systematic comparison of useful plants from other countries with the plant population of the country under consideration, and testing these plants for their quality. The second, and in the end much more important way of discovering new treasures from the plant world is by constant observation of nature, and investigations of genetical relationships. A certain amount of intuition is of course always involved. In my opinion, purely accidental discoveries are very rare indeed. The second way is much more likely to lead to the discovery of new facts, since essentially the first only treats material already known. Nevertheless, it should not altogether be neglected.

In Wadi Hafir I once observed a Bedouin woman who came to draw water from a cistern. Most likely she had walked several miles in order to get there. The water table had dropped, however, her rope was too short, and consequently her bucket did not reach the water. I was about to lend her a rope of ours, when I saw that she went to the nearest bush of *Thymelea hirsuta* and began to peel off the bark. With some of this she made her rope longer, and hauled up the heavy buckets of water without difficulty. I tested the tensile strength of the fibre myself, and found it to be surprisingly great. I had a large sample collected immediately and its subsequent chemical and physical analyses showed that here was a valuable potential cellulose and fibre plant.

Let me take another example. It is generally known that the bulbs of *Colchicum* species contain Colchicin, the demand for which is greater than the supply. Those *Colchicum* spp. from Israel that have so far been analyzed, contain a relatively large amount of Colchicin. The plants occur scattered as single individuals however, not as *Colchicum autumnale* which occurs on wet meadows in Europe in such masses as to endanger the cattle grazing there. In such conditions the collection of the plant is simple and inexpensive, and of value to the owner of the pasture. The situation is entirely different in the semi-deserts and destroyed pasture lands of Israel, however, and in the Middle East in general. Here the plants generally occur as rare, or at least as scattered individuals, and the digging of them from the hard soil is difficult, expensive and soon destroys the stand altogether. I therefore collected the flowers of the plant and sent them for chemical analysis, which incidentally was carried out by the sister of our late President, Dr Anna Weizmann. The analysis showed that the flowers contain six times as much of the chemical as do the underground parts. Consequently, the bulbs should be used not for the extraction of Colchicin, but for planting in beds, and yearly collection of the flowers. Harvesting operations are thus reduced to a minimum of labour, and the plant is saved from extinction. Perhaps most important, the plant has become a subject for breeding experiments in order to obtain strains with improved yields.

The final result of converting this wild plant into a domesticated one will no doubt still require much ecological and economic research, about the results of which I am optimistic. With these examples I hope to show how diversified are the problems of the ecologist, and how often he must combine both ecological and economic considerations in order to find the best way to utilize the treasures that nature hides in our deserts.

I am convinced that a thorough analysis of our desert flora would uncover a number of new sources of raw material. Already some are being exploited, and others are gaining prominence in the thoughts of those who are concerned with such items. It must be stressed, however, that all such efforts must be preceded by the work of an ecologist.

Let me now give a few examples of potential sources of various raw materials:

Oleagenous plants — *Citrullus Coloquintus, Cucumis prophetarum, Cucurbita* spp. from the desert parts of the U.S. and Mexico, etc.

Cellulose and Fibre plants — *Agave, Retama roetam, Thymelea hirsuta, Juncus arabicus* and the Haifa grass of North Africa, *Stipa tenacissima.*

Rubber plants — *Astragalus* species in south-west Asia, *Guyaule* from the semi-deserts of northern Mexico, *Acacias* from north Africa, and many others.

Significant progress in the search for raw material plants from arid regions has been made in Australia, and probably also in Russia. In this field, also, international co-operation will prove itself to be fruitful. I need only point out that exchange of species and varieties between arid countries and particularly between the southern and northern hemisphere alone promises to have tremendous influence on the regeneration of these lands.

So far I have deliberately not mentioned plants which grow only in oases. These form a separate topic, and have already been discussed much more than actual desert plants, both from the scientific and the economic point of view. Nevertheless, they still present many ecological problems. Some of these are involved in the planning of oasis economy; for example adjustment to the high salt concentration of the water, the amount of available water, the fluctuation of the water table, the vertical zonation of various plant associations with respect to the water table, and the economical possibilities for agriculture. The details of the zonation of Ein Ghadian, an oasis in Wadi Arabia are being measured and mapped by my department.

It is interesting that, though *Juncus arabicus* appears only in a rather small area in dense stands, my assistants Rawitz and Tadmor have found specimens growing at a height of 2.60 m. above the water table in June! I have initiated the careful collection of seeds and rhizomes from these individuals, since they exhibit an ecological amplitude far above the usual, implying a much extended area for the possible cultivation of this plant.

With the question of zonation above the water table, we enter another aspect of plant ecology where the fields of ecology, hydrology and climatology meet. In concluding I would like to make a few remarks on these questions, since the possibilities for their solution are as yet not widely enough known. In accordance with the introductory nature of this lecture I cannot go into the details. Furthermore, these new methods have been discussed at several international meetings during the last few years, and I had the opportunity to refer to them only a few months ago at the UNESCO symposium in Turkey. Here a group of new ecological methods, which enable us to measure *quantitatively* certain geo-physical values by biological means is involved. Because of the extraordinary importance of these methods, I should like to provide a summary of them.

We can differentiate between four different principal methods, all based on three fundamental natural laws:

1. Liebig's Law of the Minimum
2. The Geo-ecological Law of Distribution (*J. Ecol.* 35)
3. The Biological Rules of Climatic Extremes (*Pal. J. Bot. Rehovot* Ser. 7)

Three of the methods are based on the surprising regularity of shifts in amplitude in respect to shifts in climatic factors. These shifts in amplitude have long been known, but only recently have they been analysed by statistical and mathematical methods. Here nature shows us, and I must stress this again and again, that the vegetation of a region is a much more sensitive indicator of its climate than a collection of meteorological data describing isolated single factors. The four methods provide the key to the code we are attempting to read. Let us take the example of the Laurel tree. In the graph we can see a geographical shift in its amplitude with respect to the IE-factor, that is in relation to insulation and exposure. In areas with an annual precipitation of 600-700 mm., *Laurus nobilis* occurs only on very steep slopes with a small insolation; that is, only on steep north, north-east, and north-west slopes. Between the 700 and 800 mm. isohyetals it occurs on much less steep north slopes, and even on steep west and east slopes. Between 800 and 900mm. the Laurel occurs on south slopes with a 5° slope, and at over 900 mm. of rainfall, the IE-factor ceases to be a factor influencing the geographical distribution of the species. This indicates that the plant is already at the climatic optimum of its geographical distribution. This is a clear example of the Geo-ecological Law of Distribution. This law, in abbreviated form, states, that micro-distribution (that is the topographical distribution of a species or ecotype) is a parallel function of macro-distribution or geographical distribution, since both are determined by the same ecological amplitudes.

Next comes the method of geographical shifts in amplitude in relation to the depth of the groundwater table, and finally the method of topographical shifts in amplitude in relation to the IE-factor. The depth to the water table can be determined in a case when it is not too far removed from the ground surface: also average precipitation. Since records from rain gauges are almost always inadequate in arid regions the possibilities of exact determination of isohyetals offered by these four methods are of special significance.

My last mentioned example provides corroborative evidence, since I found out only two years after the completion of ecological tests, that I had by chance conducted my experiments in the vicinity of a rain gauge with a record of more than 20 years. After considering the coefficients necessary to correct for sandy soil and elevation, the method of overlapping amplitudes indicated that average precipitation during the past 30-40 years had been 130-145 mm. per year. Two years after the publication of these results, the record of a border station 2km. from the location of my test appeared, giving a mean annual rainfall of 136.1 mm. Since then I have had several other confirmations of the accuracy of this method.

We are coming to recognize more and more that the vegetation of each region indicates its climate with much greater accuracy and sensitivity than meteorological data. The three fundamental laws and the four applied methods teach us to decipher the code in

which the book of nature is written. Since the prehistorical times man has felt that vegetation is the most sensitive indicator of climate, but only now are we beginning to succeed in the decoding.

In less poetical form, we can say that these three fundamental laws and the four biological methods derived from them supply us with quantitative solutions of geophysical problems by plantecological means. These methods are well on their way to playing an important role in the work of making the desert areas of the earth productive. For in these areas we are very near to the limit of plant survival in general, and the plants react therefore in a most sensitive way to the minutest changes in their environment. Because of this it is much easier here than in the humid regions to exploit this sensitivity for practical purposes. Nevertheless, in this field as in so many others, there must be, of necessity, close international co-operation in order to reduce errors to a minimum, and to apply practical results on a global scale.

One thing is certain, that symposia and discussions such as we are having here at the Institute of Biology in co-operation with UNESCO, are the best way to reach this objective.

MODES 'CONTRACTÉ' ET 'DIFFUS' DE LA VÉGÉTATION SAHARIENNE

Professor Th. Monod

(*Paris*)

L'un des premiers naturalistes qui se soit aventuré dans le Sahara central, le regretté Conrad Kilian opposait dès 1925 la 'flore des pays crétacico-tertiaires sud constantinois' ou 'flore du Sahara arabe' à celle 'du massif central saharien' ou 'flore du pays targui'.

Dans le Sahara arabe: 'présence de bastes étendues de pâturages quasi permanents de Salsolacées ..., les eaux ne sont pas totalement centralisées dans les lits d'oueds ..., conservation d'une certaine humidité diffuse partant, les oueds, généralement larges et mal délimités quand il en existe, n'étant que légèrement plus humides (en surface) ..., flore ... largement répandue, diffus ...'.

Dans le Sahara targui: 'végétation persistante réduite ... en général à peu près au fond des oueds au dehors desquels on trouve le désert ..., des lits d'oueds souvent en permanence très humides, avec végétation peu désertique conservée et en dehors le désert (à moins de pluie récente, car alors il y a de l'acheb) plus absolu souvent que le désert arabe, plus dépourvu encore de plantes persistantes ..., flore persistante ... réduite, concentrée aux lits d'oueds en un réseau favorisé (et peu désertique)'.

J'insistais moi-même quelques années plus tard (1931) sur les caractères distinctifs des deux 'modes', le diffus et le contracté: 'Dans les régions à flore contractée, c'est à dire tout le Sahara central à l'exception des parties hautes de l'Ahaggar, la vie végétale est exclusivement et rigoureusement cantonnée dans les oueds qui le caractérisent et lui imposent un tracé extrêmement strict. La végétation occuppe là les lignes d'un réseau aux mailles démesurées et parfaitement stériles, entournées du grêle ruban des oueds ... Si de ce Sahara central à végétation contractée on va suffisamment loin vers le Sud à la rencontre des pluies saisonnières de l'hivernage, si l'on marche assez vers le Nord pour atteindre les pays crétacico-tertiaires, si l'on pousse assez vers l'Ouest pour toucher au rivage atlantique, ou si l'on s'élève assez haut sur les pentes de l'Ahaggar, on verra alors, peu à peu, le végétation s'évader de la prison des oueds et s'étaler sur des surfaces de plus en plus vastes: de contractée elle est devenue diffuse'.

J'ajoutais: 'L'influence des précipitations (pluie ou rosée) sur le caractère diffus ou contracté de la flore saharienne me semble évidente puisque, pour un substratum identique, on voit la flore devenir, de contractée, diffuse avec l'altitude ou la proximité des influences maritimes'.

Revenant peu après (1932) sur la même question, je précisais: 'Bien que, dans le Sud Algérien, la limite entre le Sahara septentrional et le Sahara central coïncide indéniablement, *grossissimo modo,* avec un contour géologique, séparant un pays calcaire, crétacico-tertiaire, d'un pays silico-cristallin, il ne semble nullement que le passage de la flore septentrionale diffuse à la flore centrale contractée se trouve conditionnée par la composition du sol. Le Tadmait, géologiquement très

uniforme, appartient à la fois aux deux modes (par sa partie nord et sa partie sud), les calcaires de la plage pré-tassilienne ont une végétation rigoureusement contractée, les cipolins du Tanezrouft méridional également, tandis que le mode diffus reparaît sur les sommets de l'Ahaggar, dans le Sahara atlantique, et dans le Sahara sahélien, indépendamment de la composition pétrographique des substrata'.

Rappelons enfin les observations d'un botaniste de profession B. Maire (1940): 'On sait que son climat (Sahara septentrional) présente encore une régularité relative, et qu'il reçoit, bon an, mal an, quelques pluies, surtout hivernales, qui, bien que souvent peu importantes, suffisent à l'entretien d'une végétation permanente sur tous les terrains (exception faite des sables mobiles et des substrata toxiques). Cette végétation permanente forme une steppe ordinairement très lâche, qui recouvre à peu près tout le pays, constituant une *végétation diffuse*, qui a frappé les explorateurs du Sahara par son contraste avec la *végétation contractée* qu'ils ont trouvée dans le Sahara central ... Entre El-Golea et Fort-Miribel les conditions climatiques changent; les pluies deviennent de plus en plus rares et irrégulières, ce qui a pour corollaire une modification progressive de la végétation, elles ne sont plus suffisantes pour entretenir la vie de plantes pérennantes sur tous les terrains ... la végétation permanente tand à se localiser dans les dépressions ..., l'acheb, d'autre part, ne se développe plus bien, en dehors des points à végétation permanente, que dans des stations rocheuses ou sableuses bien draînées, et permattant aux graines d'échapper au balayage par les vents. Cette localisation de la végétation est caractéristique du Sahara central, et elle ne disparaît qu'en altitudes élevées'.

'Le Tadmayt est une zone de transition; sa partie septentrionale, au Nord de Fort-Miribel appartient encore, en partie tout au moins, au Sahara septentrional; sa partie méridionale appartient incontestablement déjà au Sahara central, bien qu'on y trouve encore un certain nombre de plantes caractéristiques du Sahara septentrional'.

Notons, au passage, cette bipartition du Tadmaït, surface homogène répartie entre les deux modes pour des raisons apparemment climatiques. B. Zolotarevsky et M. Murat, en 1938, formulaient quelques remarques d'un vif intérêt, soulignant le fait que l'opposition modes diffus/contracté pourrait n'être pas due à l'influence exclusive du climat.

'On ne saurait nier la part importante qui revient aux brouillards et aux rosées dans la répartition relativement régulière de l'humidité que l'on observe au Sahara septentrional et occidental cependant, la rareté des affleurements cristallins dans le premier domaine semble aussi fortement responsable de la prédominance du mode diffus de la végétation et surtout de la richesse moindre, comme le remarque Th. Monod, de ses stations privilégiées.

'Dans le Sahara méridional, au contraire, les pénéplaines et les massifs cristallins, grâce à leur imperméabilité, canalisent et localisent l'eau de pluie; ce sont ces facteurs topographiques et édaphiques qui y déterminent en premier lieu le mode contracté de végétation.

'Dans la partie sud du Sahara occidental on voit se superposer la végétation qu'on appellerait contractée, si elle existait seule, comme au Sahara méridional, et

la steppe à Salsolacées typique du Sahara septentrional. La première est favorisée par la structure géologique et la topographie du pays, la seconde par les brouillards venant de l'océan ... La strate arborescente du Sahara est toujours contractée, la strate suffrutescente est souvent diffuse et la strate des thérophytes l'est presque toujours. Le mode contracté de la strate arborescente et en partie de la strate suffrutescente est provoqué par les conditions topographiques et édaphiques, le mode diffus, quand il se rencontre, est déterminé principalement par les conditions climatiques'.

Il ne sera peut-être pas inutile de revenir sur ces diverses conclusions, d'autant plus interessantes qu'elles émanent de biologistes possédant une expérience personnelle étendue des régions en cause.

(1). *Le mode diffus est déterminé 'principalement' par le climat, mais la nature du sol peut en être aussi 'fortement responsable', les terrains crétacico-tertiaires du Sahara septentrional favorisant la diffusion, le Précambrien (pénéplaine et massifs) déterminant 'en premier lieu' la contraction, à la fois semble-t-il par leur nature (édaphisme) et leur morphologie (topographie).* — (Je n'ai pas l'impression que la nature géologique du substratum soit en cause puisque l'on peut voir (a) le mode diffus sur du Précambrien (bordure sahélienne, Sahara atlantique) ou sur des grès (*ibidem*), donc sur un substratum identique à celui des tassilis à mode contracté du Sahara central, (b) le mode contracté sur les terrains les plus variés et, fréquemment, calcaires (Hamadas Safia et El Haricha de Taoudeni, calcaires dolomitiques de l'Adrar de Mauritanie, etc.).

Ce qu'il faut, par contre, reconnaître, c'est que, à l'échelle régionale, donc pour des conditions climatiques identiques, la tendance à la décontraction croît avec le degré d'ensablement: dans l'Adrar de Mauritanie, si les versants abrupts, talus d'éboulis, etc, sont nus ou presque, les plateaux gréseux, horizontaux où modérément inclinés, dès qu'ils sont suffisamment ensablés peuvent supporter une végétation diffuse (thérophytes, hémicryptophytes, chaméphytes).

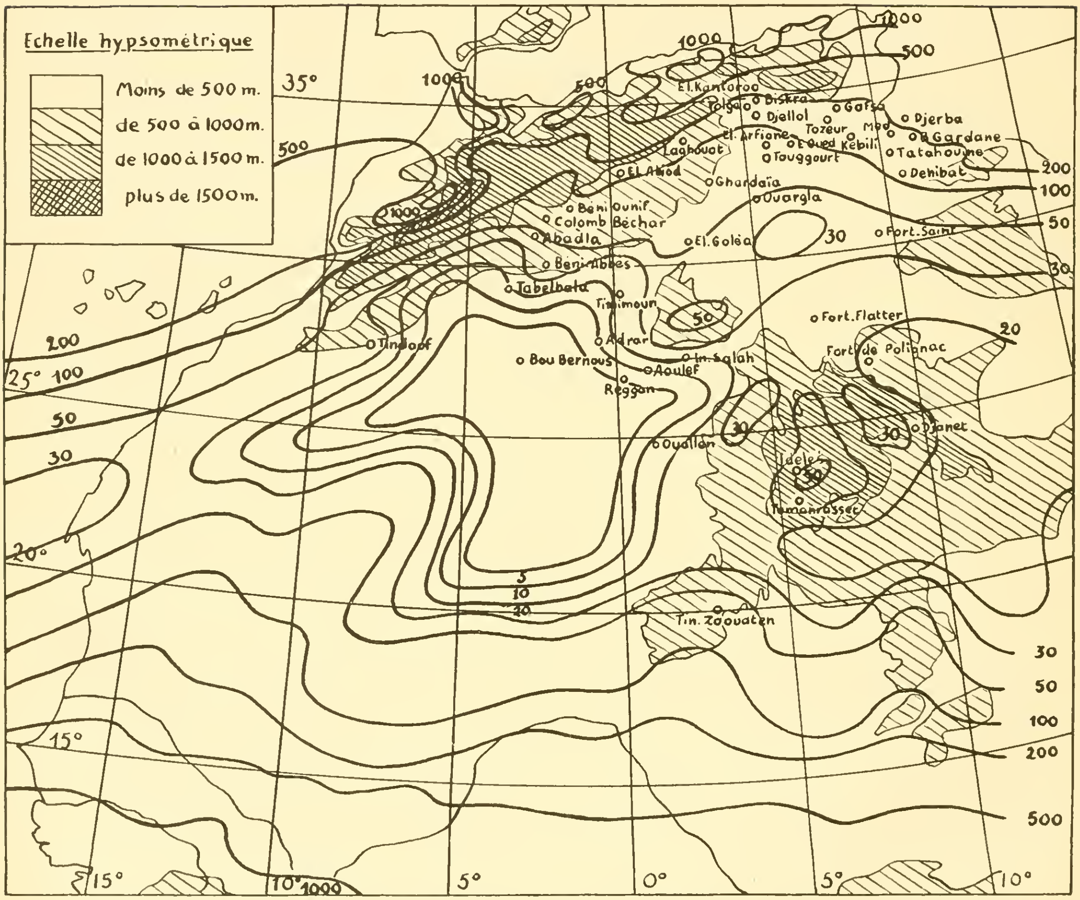
(2) *Le Sud du Sahara occidental présente une intrication, et comme une superposition des deux modes, liés l'un au climat l'autre à la physiographie (édaphisme + topographie).* — Le fait est, bien entendu, parfaitement exact et j'ai moi-même (1938) signalé l'existence d'un mode diffus (intéressant non seulement des hémicryptophytes mais des phanérophytes) sur le plateau gréseux de Chinguetti, donc sur les mêmes grès, exactement, qui supportent au Sahara central une végétation contractée.

Nous nous trouvons ici, à mon avis, sensiblement à la limite, fort imprécise évidamment, de trois territoires bioclimatiques, comme d'ailleurs de trois domaines floristiques, l'Adrar appartenant à la fois au Sahara méditerranéen et au Sahara africain*, avec des irradiations sahéliennes, et il ne serait pas, à mon avis, surprenant que la juxtaposition des deux modes ne puisse relever, ici encore, des seuls facteurs climatiques.

*cf. Monod, Th. 1952. Contribution à l'étude du peuplement de la Mauritanie — Notes botaniques sur l'Adrar de Mauritanie, (Sahara occidental) *Bull. IFAN*, **14**. (sous presse).

PLUIE TOTALE

TOTAL ANNUEL MOYEN EN MILLIMETRES



Projection conique conforme Echelle 1/20.000.000 aux latitudes 30^{0} et 60^{0}

Figure 1.

Pluie totale au Sahara (moyenne annuelle en millimètres) d'après J. Dubief et J. Lauriol, 1943, *Trav. Inst. Météor. Phys. Globe Algérie*, fasc. 4, C. 49. La limite entre le mode diffus et le mode contracté passerait approximativement vers les isohyètes de 30-50 mm (souvent entre 50 et 100 sur la bordure sahélienne).

(3) *La strate absorescente est toujours contractée, la suffrutescente souvent diffuse, celle des thérophytes presque toujours.* — On doit savoir gré à MM. Zolotarevsky et Murat d'avoir enrichi la notion des modes d'une distinction des types biologiques interessés. Il semble bien, en effet, que les modes concernent avant tout la végétation 'permanente', à l'exclusion des nappes de thérophytes pouvant se superposer aux végétations diffuses ou se juxtaposer aux contractés. Le mode diffus typique est — sauf au Sahel bien entendu — principalement constitué de chamépjytes (et d'hémicryptophytes avec la 'steppe' extra-saharienne à Halfa) alors que les phanérophytes caractérisent le mode contractée, en le colorant d'une tonalité résolument africaine.

Ajoutons toutefois que non seulement au bord sud, avec le Sahel, mais même en situation saharienne sur certains plateaux ou certaines plaines argileuses ou sablonneuses du Sahara occidental la 'décontraction' climatique ou édaphique, peut intéresser les arbres.

(4) *Le mode contracté relève de facteurs non climatiques.* — Je n'en suis pas convaincu et expliquerai plus bas pourquoi.

Quand les modes sont typiques, ils sont nettement distincts.

(1) *Mode diffus:* pseudo-steppe ou savane désertique très lâches mais recouvrant à peu près uniformément tout le pays, sans contraste très brutal entre les oueds et le reste du pays.

(2) *Mode contracté:* pseudo-steppe et savane désertique, limitées aux thalwegs, lignes de verdure incrustées dans un paysage dénudé.

Le mode diffus comprendrait les types suivants:

I *Type marginal*
- (a) Nord: ex.: pseudo-steppe à Salsolacées, etc, de Ghardaïa — El Golea.
- (b) Sud: ex.: fructicée à *Calligonum commosum, Euphorbia balsamifera,* etc., de l'Amonkrouz, Savane arbustive à *Leptadenia Spartium, Panicum turgidum, Aristida* spp., *Cenchrus biflorus,* etc., de l'Azaouad. La question se pose de savoir si, ces formations étant en fait déjà sahéliennes, il existe un type diffus marginal sud vraiment saharien.
- (c) Atlantique: ex.: pseudo-steppe à *Nucularia perrini* du Tiris.

II *Type altitudinal*
Etages méditerranéens du Hoggar et du Tibesti.

III *Type d'épandage*
Il arrive que l'on observe, au débouché d'un oued en plaine, au sortir de la montagne, ou parfois même fort loin de tout relief important en un point où un oued, à bout de course, étale largement et ses alluvions et son humidité, des zônes d'épandage parfois très vastes (mâader, grara), sablonneuses ou sablo-argileuses où la végétation, contractée plus en amont, devient typiquement diffuse.

Il arrive aussi, au moins sur la périphérie, que la diffusion apparaisse liée au sable encore mais alors que dans la cas du mâader il s'agissait d'une nappe

sablonneuse enrichie en eau par un sous écoulement, ici le revêtement arénacé, recouvrant par exemple une surface rocheuse, n'a reçu que l'apport direct des précipitations, suffisants pour nourrir, au moins temporairement (il s'agit de thérophytes ou d'hémicryptophytes plus au moins 'cycliques' et quasi 'reviviscents') une végétation diffuse.

On pourrait donc distinguer dans le type d'épandage deux sous-types:

(a) de mâader (ou grara), à alimentation souterraine, indirecte; sables épais.

(b) de plateau ou de reg, à alimentation pluviale directe; sables en revêtement mince.

Dans le mode contracté, je serais disposé à distinguer:

I *Type planitiaire*

Le mode contracté n'est pas l'apanage exclusif des massifs aux oueds encaissés; il se rencontre, sous une forme moins frappant sans doute, mais non moins typique, en plaine, et quelle que soit la nature géologique du substratum, sur une énorme surface s'étendant en latitude du Tadmaït (Sud) au Sahel (montagnes exceptées: mode contracté encaissé + mode diffus) et vers l'Ouest jusqu'à l'Adrar*. Il n'est pas de reg, de surface rocheuse sédimentaire ou de pénéplaine cristalline qui ne développe, si péniblement marqué soit-il, un chevelu hydrographique, mais la plus légère dénivellation suffit, sous le climat adéquat, à emprisonner la plante sur les lignes mêmes du ruissellement.

Ch. Sauvage avait noté, au Sahara occidental (1949, p. 45-47) que la pseudo-steppe à *Nucularia, Traganum, Salsola,* etc., ne se trouvait pas sur des regs, mais sur des zones d'épandages — parfois remarquablement plates et larges — de certains oueds, où l'on assiste évidamment à une décontraction de la végétation.

II *Type encaissé*

C'est le cas exemplaire, et classique, l'oued entaillé, souvent en canyon, et jalonné d'un ruban de verdure relativement luxuriant. Intercalé entre la diffusion altitudinale et la contraction planitiaire ce type peut être séparé de cette dernière, dont ne le distingue en fait qu'une question de degré dans le volume de la végétation, par des zones d'épandage de mode diffus. Le passage direct du type encaissé au type planitiaire ne s'observe que là où le ravin, de peu d'importance, ne provoque pas, à son entrée en plaine, d'anévrisme de type mâader.

III *Type de cuvette*

Un étalement de l'humidité en milieu contracté déclanchait, localement, une diffusion. On ne s'étonnera pas qu'un enrichissement local de l'humidité en milieu diffus ne provoque l'apparition de taches de contraction. Il semble bien, en effet, que l'on puisse à juste titre regarder comme relevant encore,

*Là où le substratum admet un ruissellement organisé, donc à l'exclusion des immenses surfaces dunaires, dont nous ignorons d'ailleurs encore le type de végétation, il meme des plateaux ensablés à mode diffus.

fût-ce sous un aspect un peu aberrant, du mode contracté des végétations de cuvettes comme celles des dayars à Pistacia-Ziziphus du Sahara algérien, ou comme celles des graras du Sahara espagnol septentrional.

Le tableau schématique des subdivisions proposées s'établirait ainsi:

ORIGINE		
Mode	climatique	physiographique
diffus	I. marginal 1D1 (a) Nord : D1*a* (b) Sud : D1*b* (c) atlantique : D1*c* II. altitudinal : D2	III. d'épandage : D3 (a) de mâader (ou grara) (b) de plateau (ou reg)
contracté	I. planitiaire : C1 II. encaissé : C2	III. de cuvette : C3

Comme on le voit, ne relèvent pour moi de la physiographie, en constituant des types localisés que les types D3 et C3.

Celui-ci concerne une contraction par *concentration* locale de l'humidité, celui-là une décontraction par *étalement* de l'humidité, par exemple au débouché en plaine d'un bassin versant. Expliquer la contraction de la végétation tassilienne, par exemple, par la topographie, ce serait admettre que le climat local, dans l'hypothèse (plaine, plateau non draîné) où l'eau ne serait pas canalisée par le réseau des oueds, permettrait l'établissement du mode diffus et que c'est la soustraction à l'ensemble de la surface, par l'écoulement encaissé linéaire, d'une part appréciable d'humidité qui dénude les interfluves et peuple les thalwegs. Or (1) là où le plateau existe plus ou moins horizontal et (2) dans les plaines adjacentes au relief (il ne s'agit pas de montagne vraie, bien entendu, celle-ci admet climatiquement, le mode diffus) et apparemment de climat comparable, on ne voit rien autre, qu'un mode contracté, très appauvri sans doute, mais typique et dont la végétation parfois relativement exubérante ('sahariennement' parlant!) des thalwegs ne représente qu'un cas particulier. Entre le véritable boisement qui occuppe le lit du canyon et le misérable 'ouedaillon' qui serpente sur le reg à peine souligné par quelques touffes espacées de Graminées, il n'y a, à mon a vis, qu'une différence de degré dans les résultats botaniques de la concentration de l'humidité, mais aucune de nature: la morphologie peut concentrer plus ou moins d'eau dans les oueds, et provoquer des variantes locales du mode contracté: l'ensemble paraît relever, quand même, d'un type de climat impliquant la contraction.

Il est à peine utile de rappeler que, si l'opposition entre la pseudo-steppe diffuse du Nord des Territoires du Sud Algérien et la savane contractée des canyons tassiliens est très marquée, il existe entre ces aspects extrêmes toute une série ménagée de types intermédiaires et puis des cas où le diagnostic sera difficile. Comment définir, par exemple, la végétation de la Hamada de Tindouf, avec des

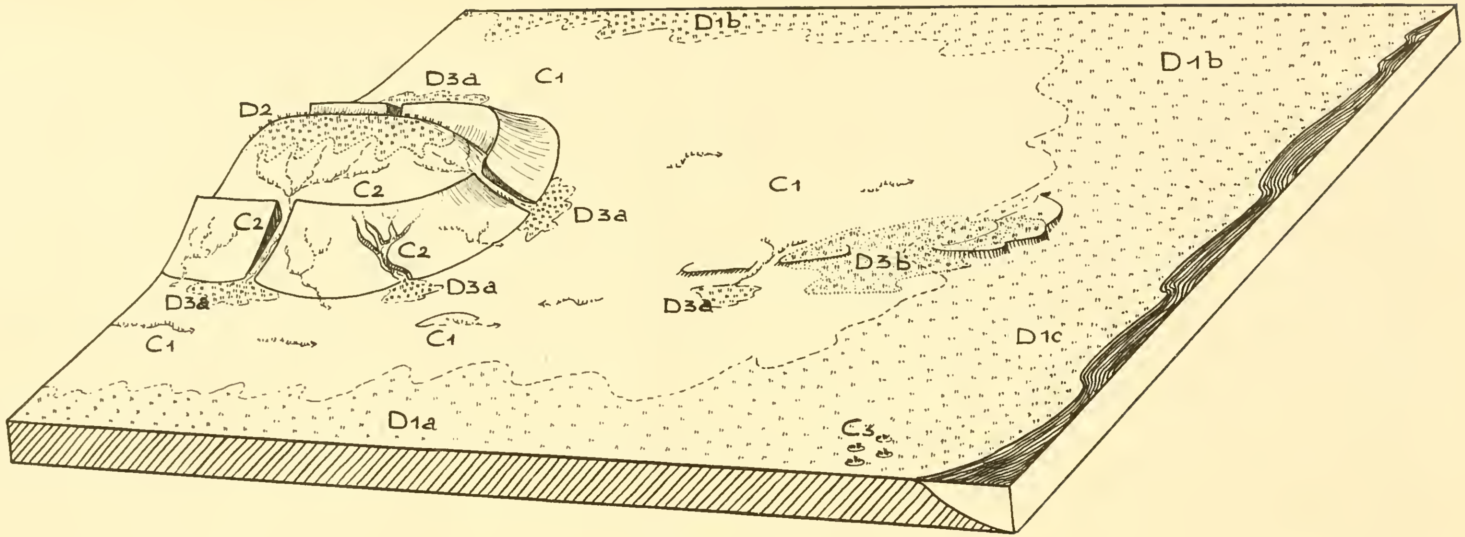


Figure 2.

Schéma perspectif de la distribution des modes au Sahara central occidental (voir dans le texte, p. 41, l'explication des signes).

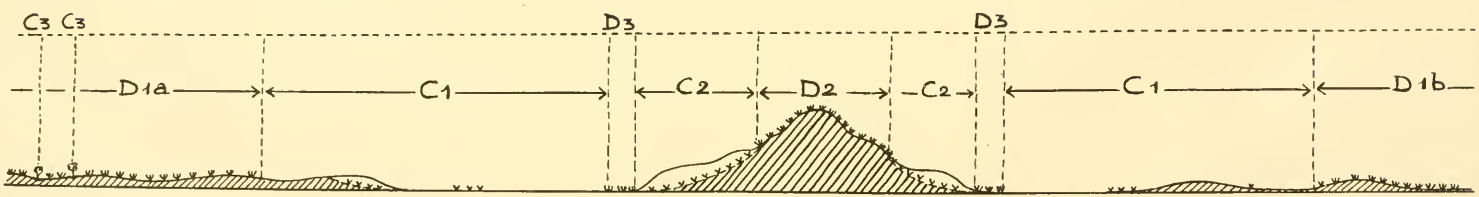


Figure 3.

Coupe schématique méridienne du Sahara, passant par le Hoggar (voir dans le texte, p. 41, l'explication des signes).

Acacia tortilis dispersés mais liés, localement, à la présence de petites cuvettes très plates. Si, comme, il le semble, cette disposition est comparable à celle des dayas à *Pistacia* du Sud Algérien, on pourrait peut-être classer dans C3 les boisements de la Hamada de Tindouf, le reste du peuplement (*Anabasis*, etc.) étant, là où il existe, diffus.

Il n'est guère possible de définir de façon tant soit peu précise, et sur des critères directement applicables sur le terrain, les deux modes là où ils peuvent se trouver au contact et atypiques, par exemple dans des secteurs de transition. D'autre part une 'bonne année', pluvieuse peut jeter sur le pays le plus aride le manteau polychrome d'une explosive floraison. La végétation de l'Adrar mauritanien dans l'hiver 1951-1952, à la suite de fines pluies, était dans une large mesure diffuse. Mais, en même temps, temporaire. Or l'essentiel de la distinction 'contraction' 'diffuse' doit porter avant tout, bien entendu, sur la végétation permanente (phanérophytes, chaméphytes, hémicryptophytes) ou semi-permanente.

A propos des écoulements en nappe en pays subarides, Cailleux distingue, de la montagne à la plaine, 4 sections*.

(a) En nappes minces sur les versants.
(b) Concentration linéaire dans les thalwegs.
(c) En nappe au débouché des deltas dans la plaine.
(d) Légère tendance à la concentration, regroupement en ébauches de petits torrents linéaires élémentaires.

On ne saurait ne point être frappé par le parallélisme de ces divisions avec les les nôtres, les sections (a), (b), (c), (d), de Cailleux paraissant correspondre à nos modes D2, C2, D3*a*, et C1.

Sans doute ne devra-t-on point trop pousser la comparaison puisque

(1) les sections de Cailleux se succèdent sur un profil d'extension limitée, et à l'intérieur d'un climat unique, à pluviosité (quantité et type) caractéristique dont elles traduisent le mode d'action au sol.

(2) mon type D2 relève de causes climatiques plus variées que l'étalement de la pluie en nappe sur 'les versants' et d'ailleurs, intéressant de vastes régions tabulaires ('tarsos' du Tibesti, etc.), elles-mêmes coupées de thalwegs, comprend à la fois des versants, des surfaces et des oueds.

(3) L'écoulement en nappes sur versants rocheux me paraît devoir être plus fréquent encore sur les pentes *nues* du domaine C2 que sur celles de D2, moins glabres.

Il n'en est pas moins intéressant de reconnaître pour deux séries différentes de manifestations, type d'écoulement, modes de végétation, cette sorte de pulsation rythmée qui, loin d'être l'apanage des choses de vie, a sans doute de bien plus vastes implications.

En tous le cas, ici: a (nappe) – b (linéaire) – c (nappe) – d (linéaire) (Calleux) et mélodie plus étendue encore si on ne la limite pas aux reliefs et à leur piémont: D1*a* – (C3) – D1*a* – C1 – D3 – C2 – D2 – C2 – D3 – C1 – D1*b*.

*Cailleux, A. 1950, *Rev. Géomorphol. Dynamique*, I, (6), 257, 261.

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THE BAHRAIN ISLANDS AND THEIR DESERT FLORA

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(Hull)

The Bahrain Islands lie some 20 miles from the coast of Saudi Arabia, about half way down the southern shore of the Persian Gulf, in the bight between Hasa and the Qatar Peninsula, at approximately 26°N and 51° E. The group consists of Bahrain Island itself, which has a length of about 30 miles and a maximum width of about 10 miles; three much smaller islands (Muharraq, Sitra and Nabbi Salih), so close to Bahrain on the north-east as to be virtually part of it; three other small islands (Umm Nasan, Jedda and Raka) more detached in the north-west; and a few tiny islets. All but the last of these are shown in figure 1.

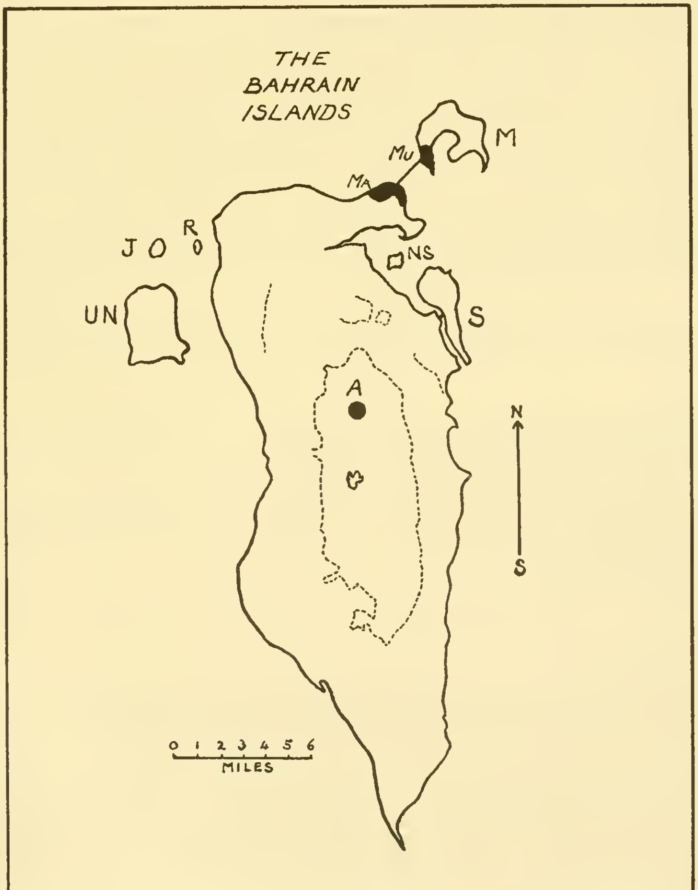

Figure 1.
Sketch map of the Bahrain Islands showing Bahrain itself and its six satellite islands, Muharraq (M), Nabbi Salih (NS), Sitra (S), Umm Nasan (UN), Jedda (J), and Raka (R), and its three towns Manama (Ma), Muharraq (Mu), and Awali (A).

Politically the archipelago is an independent Arab principality ruled by a dynasty established towards the end of the eighteenth century. The principality is in special treaty relations with the British Government, which maintains a Political Agent in Bahrain and has lately transferred there the headquarters of its Political Resident in the Persian Gulf. Bahrain is the centre of a pearl-fishing industry of great age; it has an important oil-field; and it is becoming an increasingly significant centre of air and other transport. It is also renowned for the great numbers of sepulchral mounds or tumuli which cover considerable parts of its surface and which are generally thought to be between three and four thousand years old. The population is mainly concentrated in the two coast towns of Manama and Muharraq and at a recent cencus amounted to about 120,000.

Climate

The Bahrain Islands have a remarkable and somewhat notorious climate in which the chief characteristics are high summer temperatures; scanty and irregular rainfall; high relative humidity; and rather persistent, though rarely very violent, wind. There are recording stations at Muharraq Airport and at the Bahrain Petroleum Company (BAPCO) desert town of Awali, and there is probably sufficient information available for a detailed study of conditions, but for the present purpose they may be illustrated by the following sample figures, based, unless otherwise stated, on the year 1947.

The mean annual temperature is about 80°F, or perhaps a little more, and the extreme temperature variation during the year is about 70°F. Monthly figures are:-

Average	J.	F.	M.	A.	M.	J.	J.	A.	S.	O.	N.	D.	aver.
daily mean	65	65	73	82	90	92	90	90	85	82	82	74	80
absolute max.	80	78	91	108	116	117	114	111	103	100	96	93	101
absolute min.	48	47	55	64	72	76	76	74	68	67	64	47	63

The average annual rainfall for ten recent years is 2.46 inches but the total varies greatly from year to year as shown by the 1946 figure of .15 inch and that of 1940 which was 5.53 inches, or nearly forty times as much. Rain falls on an average of about 20 days a year and there is practically none between late April and November, the monthly figures for 1947 being:-

J.	F.	M.	A.	M.	J.	J.	A.	S.	O.	N.	D.
.3	.6	.2	–	.1	–	–	–	–	–	.7	.1

The relative humidity ranges during the year from 0 to 100% and in 1947 the average daily maximum was 83% and the average daily minimum was 25%. The lowest daily maxima were 38% on 4 December and 54% on 3 June; the highest daily minima were 74% on 19 March and 70% on 8 January and 18 February. 100% was reached on 21 occasions in February, October and November (compared with 100 occasions, nearly all in the latter half of the year, in 1949), and the daily range varied from 4% on 19 March to 85% on 18 September.

There is a fairly constant light to moderate wind apparently throughout the year which comes prevailingly from the northern quarters and especially from the north-west. This wind is commonly called a *shamal* locally and tempers the climate, while the rarer southerly winds tend to be oppressive. During the first seven months of 1947 there was,

at some time every day, a wind of at least 10 miles an hour, and on two or three occasions the daily minimum was 20 miles per hour, but some calm periods were recorded on most days. The absolute maximum rate during this period was just over 50 miles per hour.

Bahrain Island

1. *Structure and physiography.*

Geologically Bahrain Island is a simple shallow elongated anticlinal dome of Eocene rocks, which dip down-flank from 1 to 5 degrees, and which are covered peripherally and unconformably by more recent deposits. On the north this peripheral extension of the island is considerable and mainly of rocks of Miocene age with a maximum thickness of about 150 feet but these are partially or entirely covered with even younger superficial deposits. The Miocene – Eocene boundary runs through the north part of Sitra, across Nabbi Salih to Adari and Barbar. In this part also the island appears to be growing by the gradual elevation of fringing coral reefs. In the south the peripheral extension is even greater and again consists largely of Miocene rocks, with a thickness of some 90 feet, but these are completely covered with younger deposits. Here there are no coral reefs and the island tapers abruptly at its south end to a sharp point of small sand-dunes. On the west the peripheral belt, though similar, is much narrower and there are no reefs. Here again there is evidence of recent uplift in the presence of a raised beach. On the east the peripheral belt is lacking for a distance of some miles. The highest existing point of the Eocene dome, the summit of the *massif* known as the Jebel Dukhan, is about 450 feet above sea level.

Except for the peripheral deposits there are no major faults or unconformities in the island and the simplicity of its anticlinal structure is complicated in only one important respect. This complication is that the whole central part of the island, comprising an area about 12 miles by 4, is a great shallow saucer with a slightly convex floor, from which rises the Jebel Dukhan, and surrounded by a scarp cliff, called by the petroleum geologists the Rim Rock, which averages about 50 feet in height. The Jebel Dukhan is slightly west and north of the exact middle of the saucer and the floor is rather lower in the south and parts of the west (where it is not more than 50 feet above the level of the sea) than in the east and north (where it is about 100 feet above the sea). Figure 2 shows diagrammatic sections of the island along the two main axes with the vertical scale very greatly exaggerated.

In the northern part of the island there are in two places, near Buri and Al Hisi, lengths of other scarp cliffs very like those of the Rim Rock, and these are apparently all that now remains of an outer scarp cliff.

The main strata of the Eocene rocks on the island are seven, namely, from above downwards:-

1.	White limestone	0 – 150 feet thick
2.	Orange Marl	30 – 50 feet thick
3.	Brown crystalline limestone – Nummulitic limestone	100 – 150 feet thick

4.	(a) *Alveolina* zone	30 – 50 feet thick
	(b) Shark's tooth shales	6 – 8 feet thick
5.	Chalky zone	110 – 220 feet thick
6.	Central brown limestone	nowhere completely exposed

The relation of these strata to one another and to the inner and outer scarps is shown diagrammatically in figure 3.

Two explanations have been advanced to account for this remarkable structure of saucer and scarps. Pilgrim, who made the first sketch of the geology of the island (see *Mem. Geol. Survey India,* XXXIV, pt. iv, 1908) thought these features were formed soon after the island was first raised, by the ordinary processes of sub-aerial denudation operating on the various strata described above at a time when rainfall was much greater than it is now. Later the island first sank and then emerged again so that the saucer

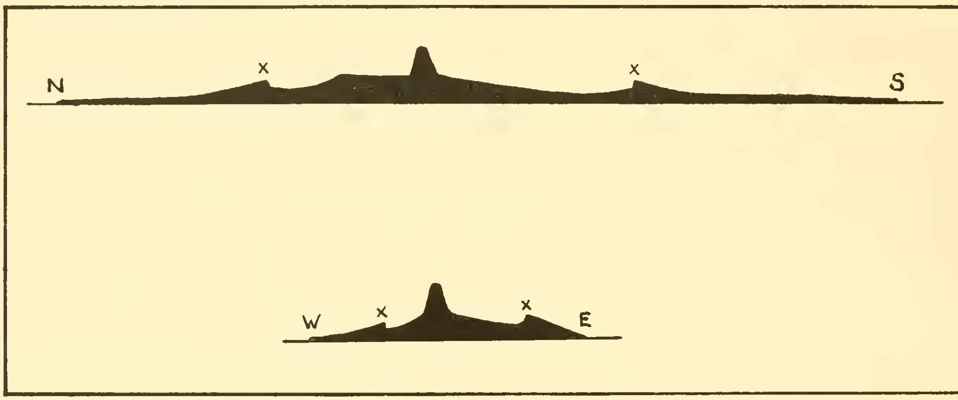

Figure 2.

Diagrammatic sections across Bahrain Island from north to south and from west to east passing through the Jebel Dukhan. The crosses indicate the Rim Rock or scarp of the central saucer. Vertical scale greatly exaggerated.

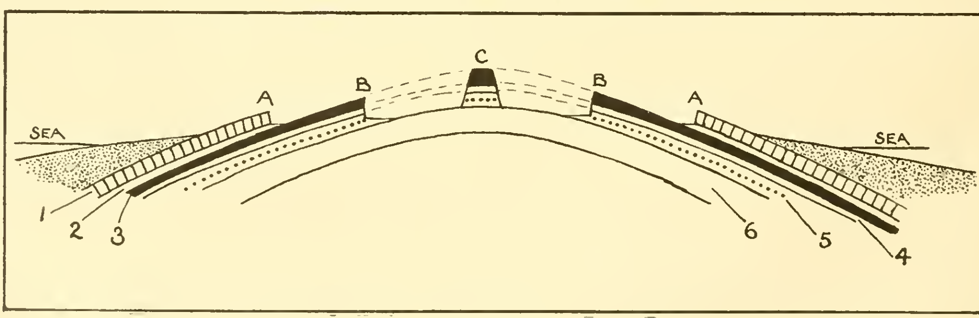

Figure 3.

Ideal diagrammatic section, not to scale, across Bahrain Island along the line Buri, Jebel Dukhan, Al Hisi to illustrate the geological structure of the island. The peripheral post-Eocene deposits are stippled; the numbers are those of the six main strata, i.e. the white limestone, the orange marl, the brown crystalline limestone, the *Alveolina* and shark's tooth beds, the chalky zone, and the central brown limestone. AA is the outer scarp of which only traces remain; BB is the Rim Rock or scarp of the saucer; and C is the summit of the Jebel.

previously formed remained as a lake, and it was the draining away of this water, mainly by way of the Zallaq gap (which is the only pass in the scarp cliff), Pilgrim suggests, that the final configuration was attained. This explanation is a little complex and is clearly based to some extent on the necessity of accounting for the sub-recent marine shells which occur in places on the floor of the saucer.

A more recent suggestion is that the saucer has been formed, at least in part, by foundering or 'slumping', that is to say by the shallow local vertical displacement of strata as a result of the dissolving out of the salts in some of the lower beds and particularly of the anhydrite which occurs in considerable quantity in the chalky zone.

These theories need not be considered in detail here but it is appropriate to call attention to two points.

Scattered over the surface of the saucer are various more or less isolated bluffs in different stages of erosion, which on a small scale are analogous with the Jebel Dukhan itself, and the outer of these at any rate are clearly detached portions of the Rim Rock, and it is not easy to see why these should have been left projecting from what was, on the first theory, a lake, or to account for them on the hypothesis of slumping. On the northern flanks of the dome (outside the Rim Rock) there are two smaller depressions, Umm Abdullah and Al Buhai, which seem clearly enough to be miniature replicas of the main saucer, though without anything corresponding to the Jebel in the middle. At Al Buhai the surrounding scarp cliff is continuous and there is no egress corresponding to the Zallaq gap, and it is difficult to imagine how the material of this excavation can have been removed by water erosion.

The essential difference between the two theories is, of course, that according to the first the filling of the saucer has been entirely removed, while according to the second it has merely been displaced *in situ*. A careful correlation of the beds of the Rim Rock, of the saucer floor and of the Jebel, should therefore afford strong evidence either for or against the hypothesis of slumping.

This correlation has been made in detail by the geologists of the Bahrain Petroleum Company and is demonstrated, by their courtesy, in figure 3. From this it will be seen that the floor of the saucer is a true floor of denudation and therefore that the material which must once have filled the saucer has been removed. It is also seen that the summit of the Jebel Dukhan consists of beds of stratum 3 (capped by resistant chert) and that the summit of the anticline was therefore once higher by at least the thickness of strata 1 and 2, which today have quite disappeared except here and there towards the periphery of the dome.

On this evidence it seems certain enough that, although slumping may have occurred here and there on a quite local scale, it cannot be made to account for the saucer as it is today, or for the formation of the outer scarp, and that a satisfactory explanation for this remarkable physical structure is still to be sought.

Rather surprisingly subterranean water is plentiful in many parts of the island, because, both in the Eocene rocks as well as in the more recent deposits, porous and more impervious beds tend to alternate, and these supplies can be tapped by shallow or artesian wells according to their depth. Most of the deeper water is said to be derived

from the rainfall of Central Arabia and even from regions further north-west, but some of the shallower wells derive their supplies from local rainfall catchment. Unfortunatel all this water (except for one or two shallow wells) is highly brackish, that from the north of the island commonly containing between two and three thousand parts per million of dissolved salts, and that from the south as much as four thousand parts. It is owing to this circumstance that despite the amount of water available for irrigation the only crops which flourish on a considerable scale are dates and lucerne.

2. *Natural Areas.*

In the simplest terms Bahrain and its three most closely associated islands consist of two natural regions only, those of the peripheral post-Eocene deposits, roughly outlined by the 50 ft. contour line, and the central Eocene dome, but each of these is further divisible.

With regard to the first various circumstances, of which the distribution and accessibility of water is probably the most important, combine to make the northern part of the area, and especially that north of the Miocene boundary, of much greater potentiality as a human habitat than the rest of the island. In consequence nearly the whole population is here and human exploitation of every sort diminishes very rapidly towards the south. In latter years it is true that the building of the oil company's desert town of Awali at the north end of the saucer has in some measure distorted this picture in fact though not in theory, since its presence there has been made possible only by overcoming the natural limitations of the site by purely artificial means.

The direction of the prevailing wind from the north-west adds a north-west to south-east component to this southward gradient, partly by its effect on the distribution of rainfall, and partly by the accumulation of blown sand in its direction. As a result there is, in addition to a diminishing human gradient from north to south a diminishing vegetational (fertility) gradient from north-west to south-east, an effect which is particularly noticeable within the saucer.

The PERIPHERAL (post-Eocene) ZONE which, it will be recalled, is absent alon the central part of the east coast, can be divided into a northern cultivated area and a western and southern almost uninhabited part. The boundary between the two in the north-west of the island is not however clearly marked since there are areas of more or less natural desert almost to the north coast, while there are scattered date gardens far to the south. The cultivated area has several aspects; the western and southern area is more monotonous, its chief feature being an extensive shallow pan running north-west from Mattala.

The CENTRAL (Eocene) DOME divides into several constituent parts in accordanc with the physiography illustrated in figures 2 and 3, namely the FLANKS; the SAUCER the CENTRAL PLATEAU and the JEBEL DUKHAN. The first of these is complex in that it is locally double where the outer scarps occur and the white limestone is expose but on the main continuous flanks outside the saucer it is the brown crystalline limestone that provides the surface, except for some local patches of orange marl. The surface of the saucer is of beds of the chalky zone, modified to a varying degree by the products of erosion of the central plateau and the Jebel. The central plateau is formed

of the central brown limestone which, superficially at least, is not very different from the brown crystalline limestone. Lastly the Jebel Dukhan consists of a base of chalky zone beds, above which are the *Alveolina* – Shark's tooth series, and the brown crystalline limestone, this last capped by a bed of resistant chert.

Both the flanks and the saucer are conveniently subdivided again, the former into four parts, north, south, east and west, and the latter into two, north-west and south-east.

These various natural areas are shown in figure 4.

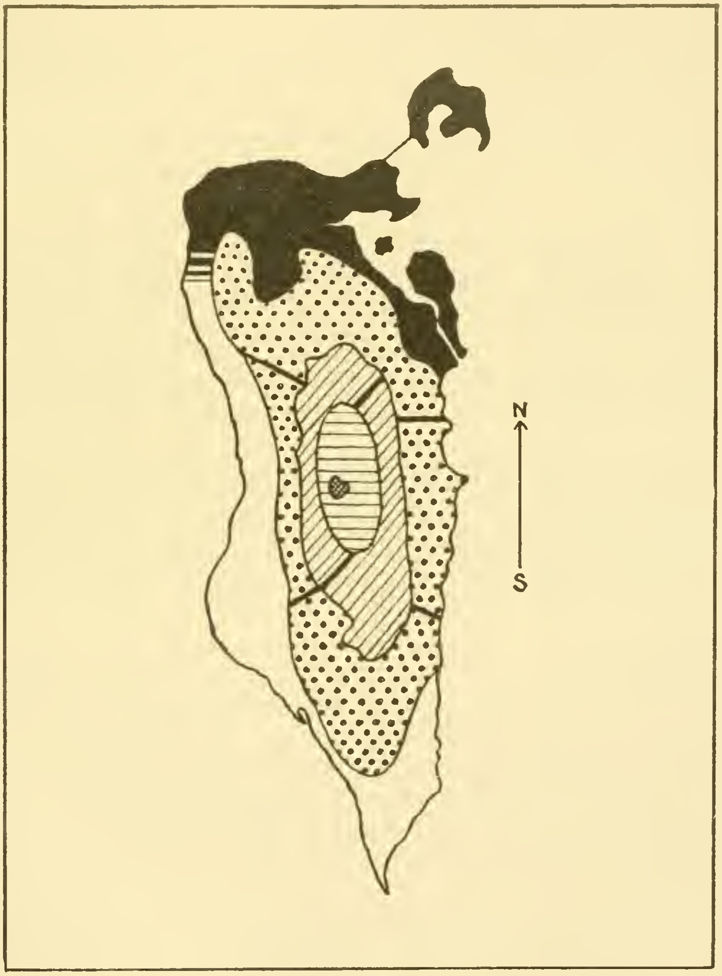

Figure 4.

Sketch map showing the natural areas of Bahrain Island, as follows:-

Peripheral Zone. Northern peripheral area (black). Western and southern area (white)

Central Dome. Flanks, divided into north, south, west and east (spotted). Saucer, divided into north-west and south-east (diagonal lines). Central plateau (horizontal lines). Jebel Dukhan (cross hatched).

3. *The Desert Vegetation*

The vegetation of Bahrain comprises three formations or major communities of species of which two are local, one of these being largely adventive.

Most restricted in distribution is the halophytic vegetation of muddy shores, namely salt marsh and mangrove swamp, which occurs especially on parts of the shores of the deep inlet a mile or two south of Manama and more sporadically near Sitra.

More extensive but still local is the mainly adventive flora of the date and other gardens in the cultivated northern part of the peripheral zone, where constant irrigation is practised.

Everywhere else on the island the vegetation is one or other minor facies of a single rich but highly selected desert plant community of the general North African – Indian desert flora, – comprising something less than 200 species. Nowhere on the island, with the two exceptions already noted, is climate, soil, altitude or any other influence sufficient to cause any real replacement or even important modification of this general plant community.

The natural desert areas of Bahrain, that is to say the whole island outside the cultivated part of the peripheral zone, displays well the three most prevalent kinds of desert habitat, namely sandy or small-dune desert; stony and gravelly desert, or *reg;* and rock exposures, or *hamada,* as well as one or two particular conditions.

A. Sandy desert, in which the substrate is so loose as to pile up to some extent at least against the larger plants, is the characteristic condition of the peripheral zone and occurs also here and there in the saucer, especially in the south-east, where wind-borne material tends to accumulate. Its vegetation is often more considerable in bulk than that of the other deserts because some of the individuals are larger (e.g. *Leptadenia pyrotechnica*) but the species are fewer and of a more halophytic sort. In one direction this type of desert passes towards plantless loose sand and in the other towards consolidated salt flats such as are found north of Mattala and here and there elsewhere.

B. Stony and gravelly desert is also widespread and, to the eye at least, is the most characteristic feature of the island, since it prevails in the more accessible parts, covering practically all the flanks of the central dome and parts of the central plateau. The surface is of more or less consolidated sand or marl, thickly or even completely covered with irregular and angular pieces of flint, chert or limestone, ranging from a quarter of an inch to several inches in diameter, generally white or pale yellow but often black and frequently modified in colour by grey-green or yellow lichens, which are a conspicuous feature of these deserts. This stony desert surface is presumably the result of denudation *in situ* and it is here that the tumuli are so numerous, and from this material that they are made. The vegetation is on the whole sparse, especially towards the tops of the slopes, and there are often distances of many feet between neighbouring plants, but it becomes much thicker wherever a slight cavity or consolidation (as, for instance, wheel ruts) retains the intermittent rainfall a little longer than elsewhere. Such depressions are especially numerous between the tumuli and here the vegetation is often almost closed. The surface of the tumuli resembles that of the plain and they tend to bear a slightly depauperated mixture of the same species, with notably more individuals on their northern sides.

C. Exposed limestone is found on the flanks where intermittent surface drainage has scoured away some or all of the overlying sand and gravel, namely in the numerous small wadis which are thickly distributed here, but occurs also in parts of the central plateau where wind erosion has perhaps played a larger part. According to the steepness and nature of the substrate occasional heavy rain may pass through these wadis almost in a torrent, but elsewhere the flow may for various reasons be slower so that there may even temporarily be pools of standing water. It is in these flatter wadis that the richest and most luxuriant vegetation of the island is to be seen, in the form of thickets several feet high composed of such shrubby plants as *Zizyphus* and *Atriplex* and various large herbs and grasses. These wadis also show the largest collections of species, one of them for example, south-east of the village of Ali, containing upwards of 90 species, or about half the whole desert flora.

On the central feature of the island, the Jebel Dukhan, all three main types of desert occur; sandy desert on parts of the north slopes, where wind has deposited material, stony desert on the summits and flanks where the rock is not fully denuded and exposed, and exposed limestone on the rest of the summits and on the flanks where slope and other factors preclude any more superficial deposit. The Jebel presents two habitat features peculiar to itself and its minor homologues, namely the presence of slopes steeper than found elsewhere and locally even precipitous, and in consequence the occurrence also locally of shaded niches such as do not occur on the open desert. It is interesting to note however that while various species attain an unusual size in such favoured spots there are apparently no species peculiar to them. About 75 species occur on the Jebel.

The parts of the saucer which do not bear typical sandy desert are for the most part in something between this condition and stony desert but very notably on the west side the white, marly beds of the chalky zone are bare, and here there are large patches of vegetation of considerable local repute for horse and other grazing owing to the presence of 'sorrel' (apparently *Emex spinosus*) and certain other plants.

The Island of Umm Nasan

This has an area of about 9 square miles. It is used as a hunting preserve by the Sheikh and is inhabited only by a few of his retainers.

Apart from some very local and shallow limestone exposures on the shore the whole island is a flat sandy plain from which emerge two low isolated rocky hills of which the larger is about 70 feet high. Owing to the extreme flatness of the rest of the island these hills have a prominence out of all proportion to their size and are visible from a considerable distance.

The sandy plain compares with the peripheral zone of Bahrain and is presumably of similar age, and bears a well-developed community of about a dozen species all of which occur also on the larger island. The hills each compare with the Jebel Dukhan on a minute scale and the larger has 35 of the same species.

The Island of Jedda

This island, which is about a mile round, is used as a prison. It is a solid flat-topped mass of limestone with practically no peripheral zone and is almost everywhere

surrounded by cliffs less than 100 feet high. The surface of the island is similar to, and compares with, the summit of Jebel Dukhan as a plant habitat and has a flora of about 40 species, all represented on Bahrain.

The Island of Raka

This small island is now a private estate with much cultivation and was not visited.

The Bahrain Desert Flora

The main feature of the desert flora of the Bahrain Islands is certainly its lack of particularity. It may be that one or two of the more critical species will, on close examination prove to be peculiar to it but it is clear that there is virtually no endemic element in the flora. Not only so but considerably more than half the species are generally described as having ranges which cover at least the greater part of the whole North African-Indian desert region, and the occurrence of these in Bahrain calls for no special comment, because the islands lie close to the mainland of Arabia, which is one of the chief constituent parts of this region. There is also a considerable number of species which are usually regarded as characteristic of the western or 'Mediterranean' part of this great region, and for many of these the Bahrain records probably extend the known distribution considerably to the east. The remaining species, which do not number more than about twenty, are geographically either Arabian or Persian-Indian, that is to say they relate to one or other side of the gulf in which the Bahrain Islands lie. In short, the Bahrain desert flora may be described as essentially an Arabian flora in which the proportion of more widespread North African-Indian desert species is very high.

Probably the most generally distributed species is *Zygophyllum album* which may occur in almost any situation. Also particularly characteristic are *Mesembryanthemum nodiflorum, Heliotropium tuberculosum, Limonium axillare, Lycium persicum, Asphodelus tenuifolius, Aeluropus lagopoides, Sporobolus pallidus* and *Stipa tortilis.*

Other common and prominent plants are:-

Reseda muricata
Helianthemum kahiricum
Helianthemum lippi
Frankenia pulverulenta
Spergularia diandra
Fagonia ? bruguieri
Zygophyllum simplex
Erodium glaucophyllum
Erodium laciniatum
Astragalus tribuloides
Medicago laciniata
Trigonella stellata
Aizoon canariense
Opophytum forskahlei
Calendula aegyptiaca
Launaea mucronata
Launaea nudicaulis
Ifloga spicata
Richardea tingitana
Senecio coronopifolius
Glossonema edule
Cressa cretica
Arnebia hispidissima
Plantago coronopus
Herniaria hemistemon
Sclerocarpus arabicus
Halopeplis perfoliatus
Salsola brevifolia
Andrachne telephioides
Cyperus arenarius
Hyparrhenia hirta
Cymbopogon schoenanthus
Koeleria phleoides
Schismus barbatus

Of the less common but particularly striking plants may be mentioned *Ochradenus baccatus, Leptadenia pyrotechnica, Aerva javanica, Rumex vesicarius* and *Calligonum comosum,* and the two parasites *Cistanche lutea* and *Cynomorium coccineum.* Small individuals of the date palm, *Phoenix dactylifera,* are numerous in the sandier deserts, but it is difficult to determine their status.

The lack of endemism and the high proportion of widely distributed species in the present flora of Bahrain suggests that it is a relatively new flora, in the sense that it has not long been established in the islands, and this is of interest because it accords with the impression gained from other sources also, such as the archaeological, that the present state of the islands may be of comparatively recent origin. This again impinges on the much wider problem of the age and history of the North African-Arabian desert as a whole, which is not only one of the most fascinating questions of palaeogeography but also one to which a satisfactory answer might be of the greatest significance in that task of raising or restoring the productivity of the world's desert areas which is such a pressing urgency of our time.

The foregoing account of the Bahrain Islands and their desert vegetation has been prepared from material and specimens collected by the writer during a visit to the islands early in 1950. His thank are due to the Royal Society for the generous grant which made his visit possible, and he would also express his gratitude for the welcome and help received from His Highness Shaikh Sulman; his Adviser, Sir Charles Belgrave; from Sir Rupert Hay and other representatives of the British Government; and from Mr E.A. Skinner and others of the Bahrain Petroleum Company. For the identifications of most of the plants mentioned he is indebted to Mr B.L. Burtt, late of the Royal Botanic Gardens, Kew.

HYDRO-ECONOMICAL TYPES IN THE VEGETATION OF NEAR EAST DESERTS

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(*Jerusalem*)

This paper presents readily comparable data on the hydro-ecological behaviour of the leading species of the most common plant communities representative of the Near East deserts.

The Near East deserts comprise a vast trapezoid limited by the Syro-Palestine mountain system to the west and by the Zagros mountains to the east. In the north it merges into southern Anatoly and in the south it is bordered by a line drawn from Suez Gulf to the Gulf of Aqaba.

The climate of these deserts is an extreme variety of the Mediterranean type, characterized by mild to fairly cold and rainy winters and dry hot summers. The mean monthly winter temperature never drops below 0°C. The bulk of the area (about 80%) is situated between the isohytes of 200 and 50mm and the monthly distribution of the rainfall is very unstable.

Although rather uniform in the physiognomy of its vegetation, the area under review consists of two plant-geographical territories, the Irano-Turanian in the north and the Saharo-Sindian in the south (Eig. 1938).

The observations and measurements recorded here were made mainly in the following plant associations: Association of *Artemisia monosperma - Convolvulus lanatus* (on the eastern fringes of the coastal sand dunes); *Haloxyletum articulati* (on sandy loess); *Zygophylletum dumosi* (on hammada); *Acacietum tortilidis* (in runnels crossing sterile hammada); and *Haloxyletum persici* (on interior sand dunes derived from Cretaceous Nubian Sandstone and crystalline rocks).

Pheno-Ecology

By pheno-ecology I mean those seasonal changes in the plant organs which affect, directly or indirectly, the water economy of the plant. An analysis of the flora of the area concerned has led to the distinction of the following types (Fig. 1).

(a) *Acacia* type. Evergreen trees shedding the old leaves or green branches after the formation of the new ones, so that defoliation never occurs. Time of leaf-fall – summer.(*Acacia raddiana, A. spirocarpa, Tamarix* spp.).

(b) *Anabasis* type. Evergreen, articulate stem succulents producing new assimilating branches in winter, while certain portions of older branches die back in the summer (*Anabasis articulata, Haloxylon articulatum, H. salicornicum,* etc.).

(c) *Retama* type. Evergreen spartoids, shedding their leaves in early winter (*Retama roetan, Calligonum comosum,* etc.).

(d) *Lycium* type. Wintergreen phanerophytes shedding all their leaves in midsummer (*Lycium arabicum, Anagyris foetida,* etc.).

(e) *Reamuria* types. Chamaephytes which considerably reduce their transpiring surface at the beginning of the dry period (e.g. *Reaumuria palaestina, Salsola villosa, Suaeda palaestina, S. asphaltica, Artemisia Herba alba, Zygophyllum dumosum* and many others). This group is the most important among the permanent desert vegetation. Biseasonal annuals (e.g. *Salsola autrani*) are also included here.

(f) *Launaea* type. Annuals, crypto – or hemicryptophytes finishing their life cycles at the end of the rainy season. Very abundant.

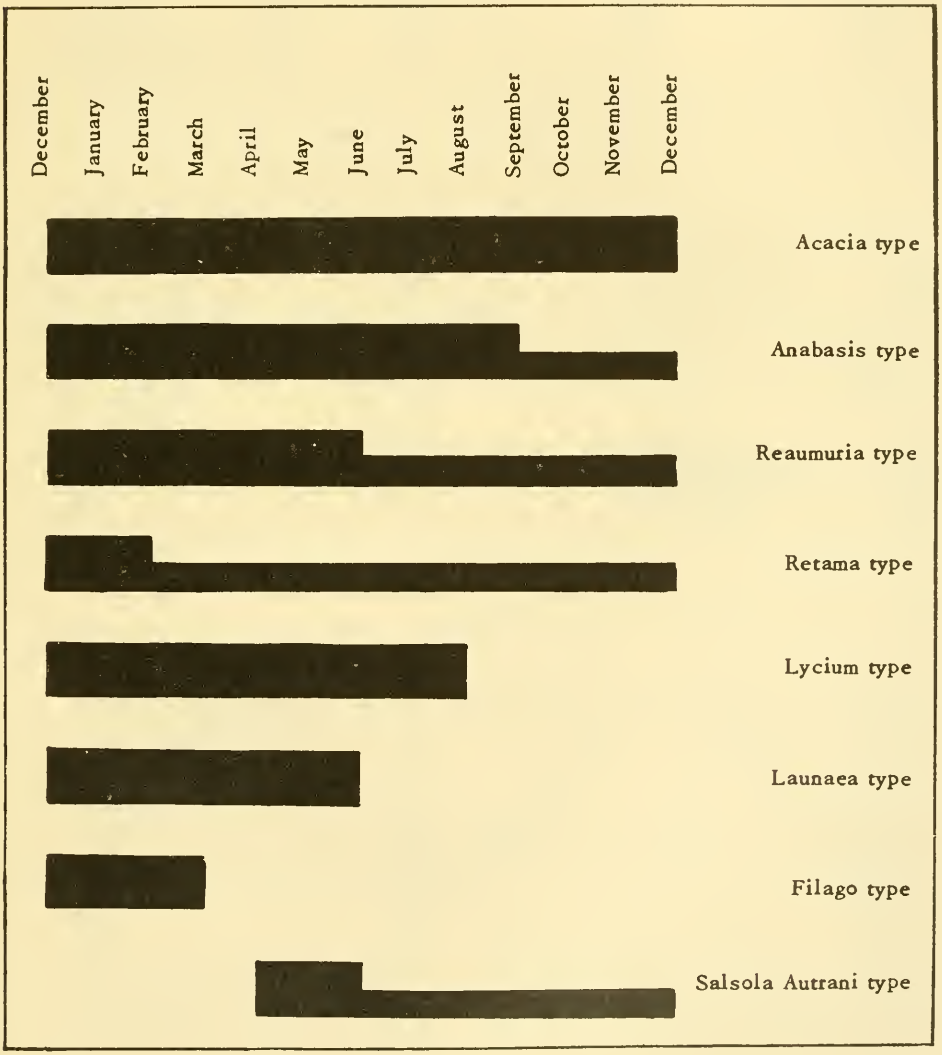

Figure 1.
Pheno-ecological types in the Near East Desert Vegetation.

(g) *Filago* type. Ephemerals finishing their life cycle long before the end of the rainy season. Very abundant.

(h) *Salsola* type. Summer annuals starting to develop in spring and shedding their large leaves in early summer, while retaining green, bract-like leaves up to the end of summer.

The above analysis demonstrates the great phenological diversity of the vegetation, and the accordance between phenological events associated with surface reduction of the transpiring body and seasonal decrease in the moisture resources of the desert.

Morpho-Ecology

By this term I refer to formal and dimensional changes in the plant body, directly or indirectly associated with its water economy. This subject also includes the study of life forms but viewed from another angle than that exposed by Raunkiaer. It is not the position and protection of the renovation buds that affect the water ecology of the plant, but the dimensions of the transpiring organs regularly lost by the plant in the critical season, that is most essential for the maintenance of desert summer vegetation. In an unpublished paper, Orshansky (1952) has shown that in the evergreen *Zygophyllum dumosum* the summer reduction of the transpiring surface amounts to $^2/_3$ of the total transpiring body. In other plants even much higher values have been found. The following morphological types have been distinguished in the local vegetation. (Fig. 2).

(a) Herbaceous whole-shoot shedders. This type comprises winter annuals, hemicryptophytes and geophytes in which the whole plant or the epigaeous part only dies away at the beginning of the dry season. This type comprises about 85% of the total flora.

(b) Phanerophytic summer leaf shedders. These include shurbs shedding the leaves in midsummer (e.g. *Lycium arabicum*).

(c) Petiolate leaflet shedders. The leaf is composed of two leaflets borne on a cylindrical leaf-like petiole, all succulent. In late spring the leaflets are shed while the petioles remain physiologically active during summer (e.g. *Zygophyllum dumosum*).

(d) Aphyllous leaf and branch shedders. This type comprises broom-like shrubs, like *Retama* spp., *Calligonum comosum*, etc., which shed their leaves in winter and remain green the year round, but in summer a part of the last year's branches dry up and break down. In this way a considerable part of the transpiring surface is removed from the plant.

(e) Aphyllous branch shedders (*Ephedra* type). They produce no leaves (except scale-like ones); a considerable part of the green and brittle branches are regularly shed in the dry season.

(f) Basiphyllous leaf shedders. At the start of the dry period the large winter leaves crowded at the base dry up and die away, while the flowering shoots develop small leaves, active during the whole summer.(*Artemisia* type.).

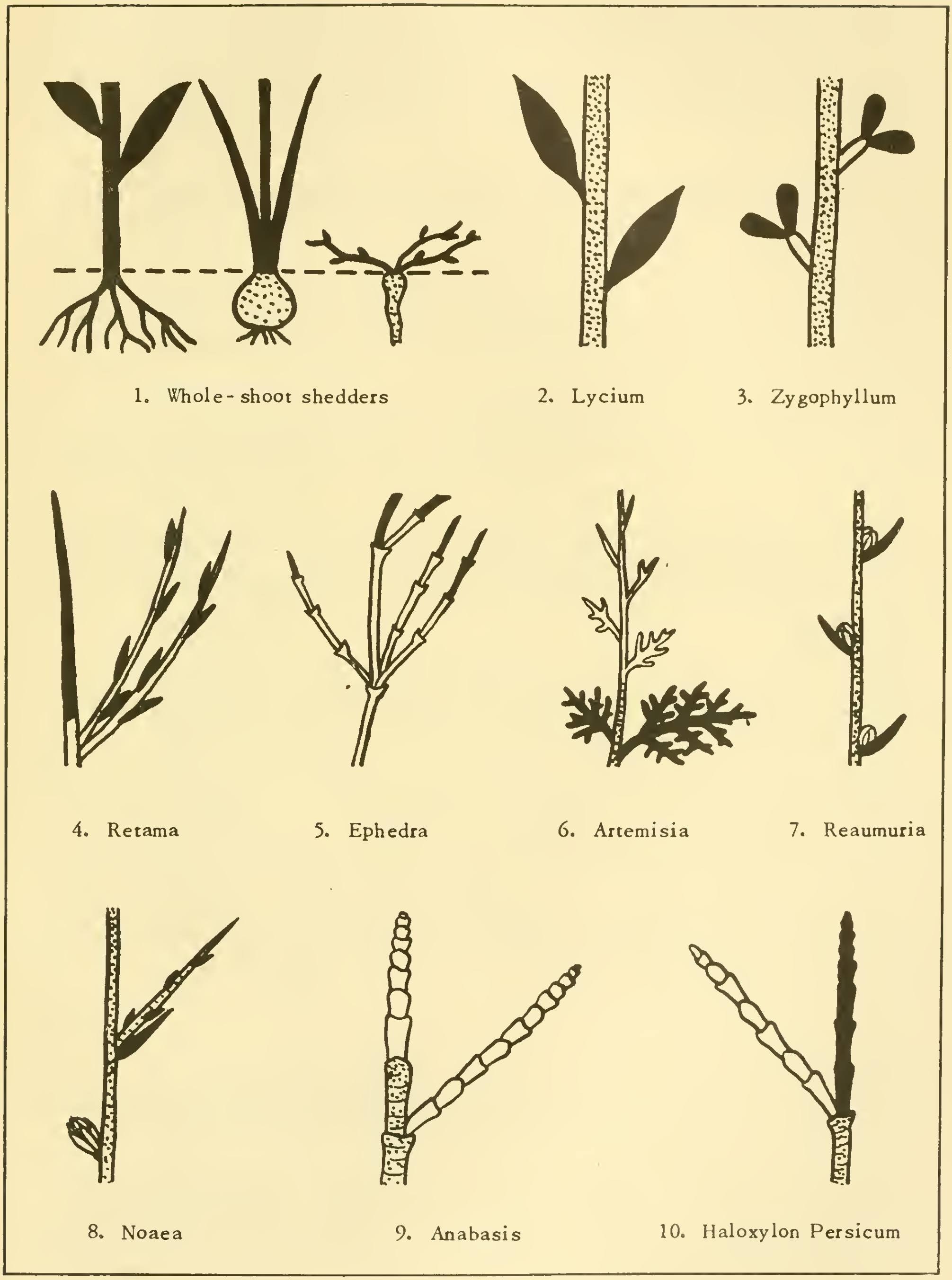

Figure 2.

Morpho-ecological diversity among the dominant species in the Near East Desert Vegetation.

(g) Brachyblastic leaf shedders. This type comprises the majority of chamaephytes, the dominant life form in desert vegetation, though constituting a small percentage only of the desert flora. The new shoots produce in the axils of the winter leaves small bud-like branches (brachyblasts) which, after the shedding of the winter leaves, are active during the whole summer (*Reaumuria* type).

(h) Aesticladous leaf shedders. In this type the brachyblasts develop in summer and consist of a spiny axis and minute leaflets, all dying away at the end of the dry season (e.g. *Noaea mucronata*).

(i) Articulate shoot splitters. These are articulate evergreen stem succulents in which considerable parts of the green 'skin' of the last year's stems are drying off and then split into rings and fall down. Here belong *Anabasis articulata, Haloxylon articulatum,* etc.

(j) Articulate branch splitters and shedders. As above but a part of the last year's branches also break down and fall away in summer (*Haloxylon persicum* type).

This way of morphological analysis renders more meaning to the life-form concept. It shows that surface reduction of the transpiring body, achieved in various ways, is most important for the permanence of the desert vegetation.

Transpiration

In order to obtain critical data on the transpiration behaviour of desert plants, measurements of transpiration intensity of the leading species of the most typical plant associations have been carried out throughout the whole year.

Transpiration has been measured by the rapid-weighing torsion balance (Huber, 1927), whereby excised plant parts have been exposed for 2-4 minutes. In most cases two or more parallel measurements with the shortest possible interval between them were made every hour for each plant. Reference has been made to fresh weight (see Huber, 1927; Walter, 1951; Hygen, 1951) and figures have been calculated to hourly averages (mg/g.h.). In order to simplify the presentation of results, data of a single summer day (in most cases August) and a typical spring day have been chosen for each plant (Fig. 3).

The conclusions from own data and those obtained by Evenari & Richter (1937) and Shmueli (1948) are:

(1) Desert plants vary considerably in their transpiration behaviour, both quantitatively and qualitatively.

(2) As to transpiration intensity two groups of plants can easily be distinguished: those with a winter and those with a summer maximum. The former includes the bulk of the permanent vegetation, while the second consists only of a few plants with extraordinarily deep roots reaching sources of permanent moisture. The fact that the dominant representatives of the permanent desert vegetation shows a considerable summer decrease in transpiration intensity, is highly significant in the water ecology of the desert.

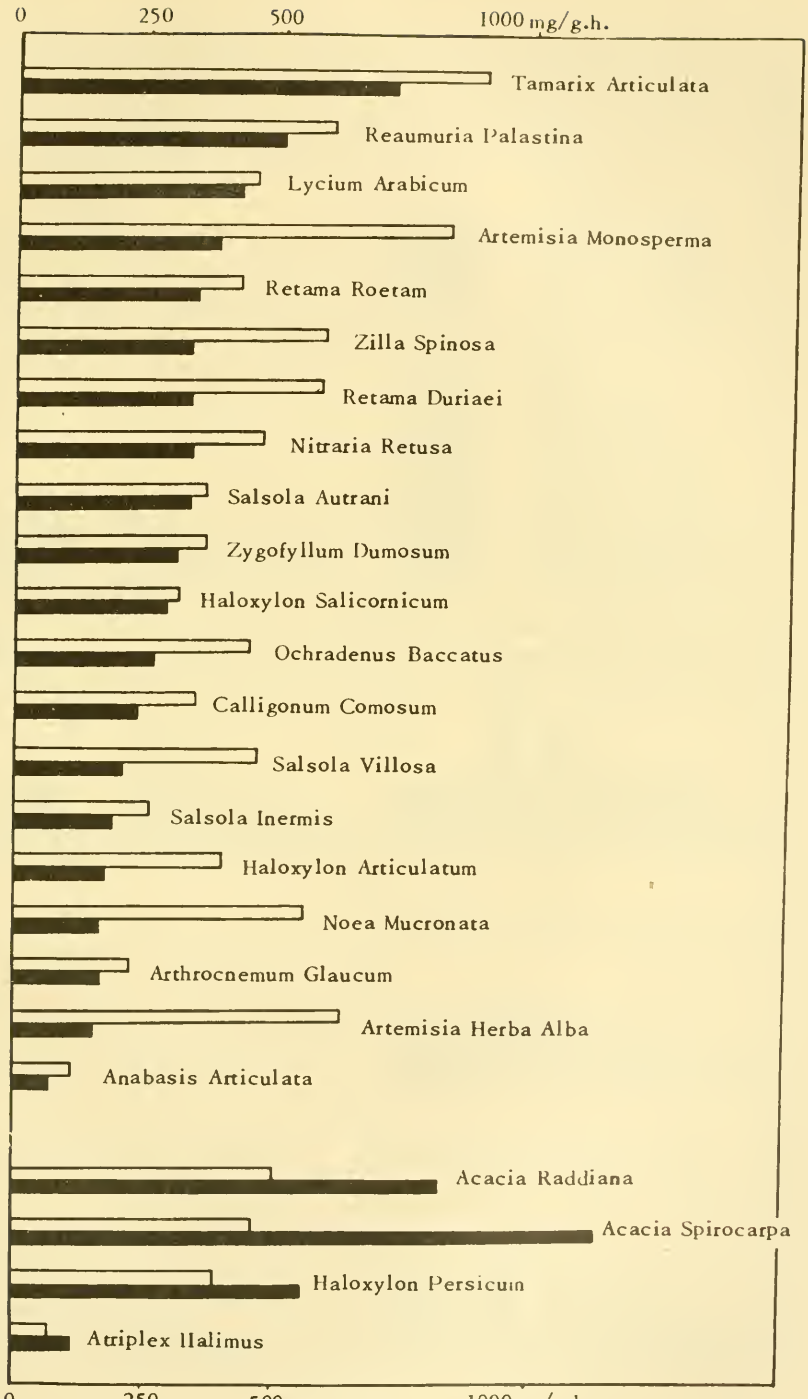

Figure 3.

Spring (white) and late summer (black) transpiration rates of dominant species of the Palestine desert vegetation.

(3) In regard to transpiration ranges, two groups can be distinguished: stenohydric plants with a rather narrow range of transpiration intensity (e.g. *Haloxylon salicornicum, Zygophyllum dumosum,* etc.) and euryhydric plants with a wide range of transpiration intensity (e.g. *Artemisia monosperma, Zilla spinosa, Retama duriaei, Calligonum comosum*).

(4) Fig. 3 indicates the distinction of three main categories of plants according to the summer values of the transpiration rate. These are megahydrics (high transpirers) from 500 mg/g.h. upwards, microhydrics (low transpirers) showing values up to 350 mg/g.h. and mesohydrics with values intermediate between both. It is clearly shown that the micro- and mesohydric types are dominant among the permanent desert vegetation while the megahydrics are rather exceptional. Indeed, only exceedingly deep rooting plants belong to the latter category.

(5) I do not agree with Stocker (1933) that there is no relation between habitat and transpiration. Fig. 4 shows clear differences in the summer transpiration rates between various plant communities. This difference is particularly striking when for each plant community one or two dominants are chosen that display the highest percentage of the permanent plant coverage, as shown in Fig. 4 (broad column). Comparing various plant communities of the desert with those of the Mediterranean region one finds striking differences between the two in late summer transpiration intensities.

Osmotic Pressure of Cell Sap

As in transpiration so also in osmotic pressure desert plants are greatly heterogeneous.

Taking the data presented in Fig. 5 as a basis, at least three groups of plants can be distinguished:

(a) Plants of hydro- or automorphous salines, distinguished by their high osmotic pressure caused by the accumulation of soluble salts in the cell vacuoles. In this group of plants the values range between 40 and 150 atm. In spite of the high pressure they are all low transpirers.

(b) Plants with low or medium summer values distinguished by their high transpiration rate and their exceedingly deep roots reaching permanent sources of soil moisture. These include *Acacia* spp. and *Tamarix* spp.

(c) The rest of the plants are true desert plants showing maxima of osmotic values between 16 and 72 atm. Comparing these values with those available for Mediterranean maquis one finds no marked differences between these and the desert plants. The following plants are particularly worthwhile mentioning: **Mediterranean**, (from Walter, 1951), *Olea europaea* (52 atm.), *Rhamnus alaternus* (37 atm.), *Phillyrea angustifolia* (60 atm.), *Lonicera etrusca* (53 atm.), *Pistacia terebinthus* (42 atm.). **Desert**, (my data), *Artemisia monosperma* (16 atm.), *A. Herba alba* (29 atm.), *Zilla spinosa* (17 atm.), *Anabasis articulata* (58 atm.), *Haloxylon persicum* (56 atm.), *Calligonum comosum* (17 atm.), *Retama roetam* (26 atm.).

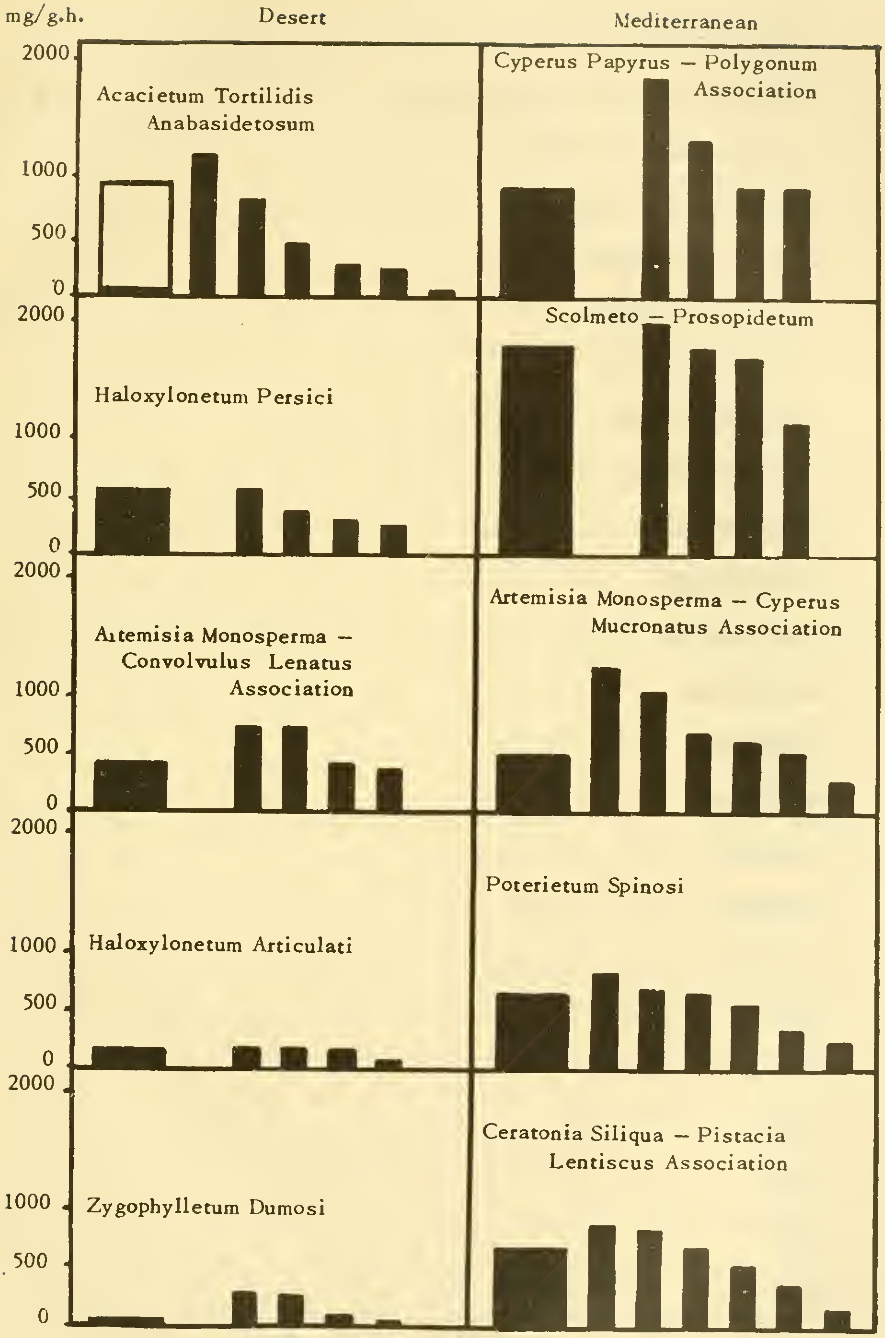

Figure 4.

Late summer transpiration rates of dominant species in typical Mediterranean and desert plant associations of Palestine.

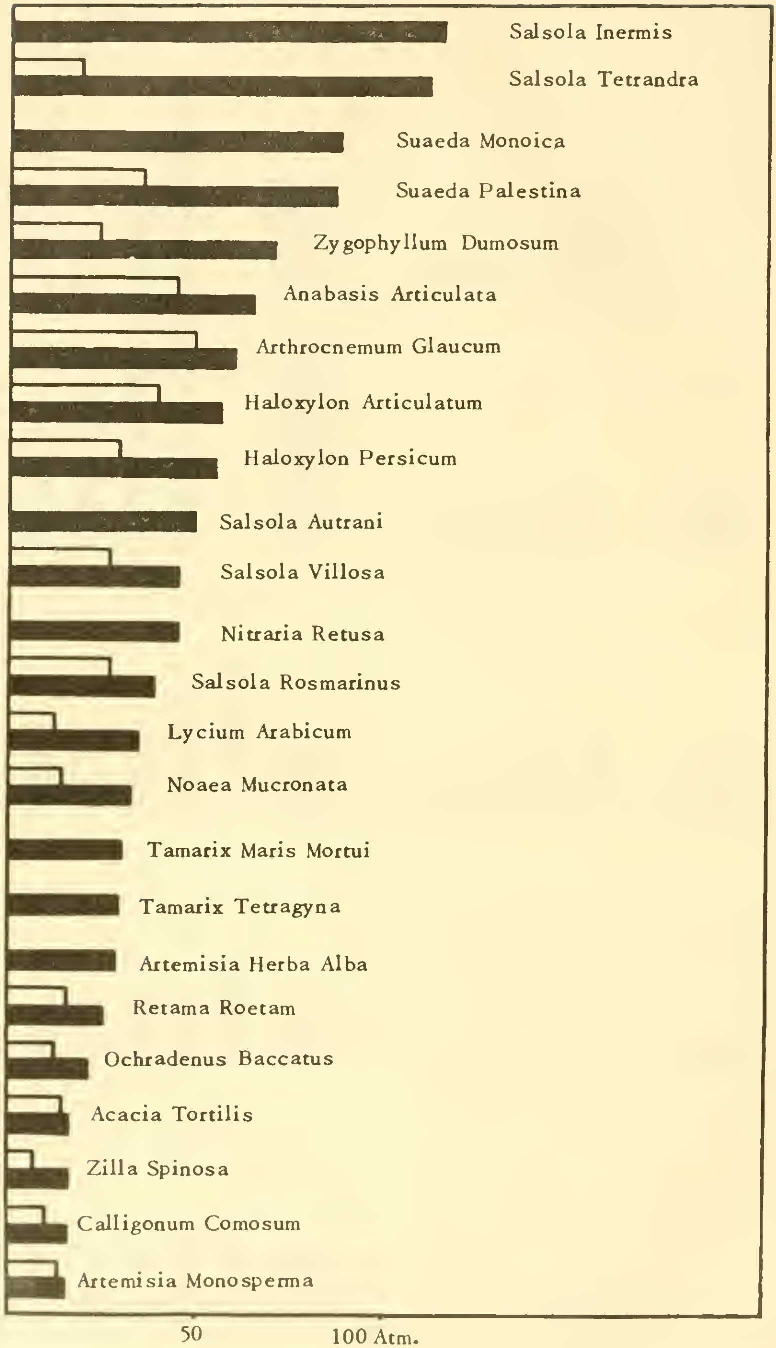

Figure 5.

Spring (white) and late summer (black) osmotic values of the dominant plants in the Near East desert vegetation.

Discussion

A glance at the literature on this subject published during the last three decades shows how inadequate and contradictory is our knowledge of the water ecology of desert plants. From the results obtained one becomes doubtful whether the older view on xerophytes, as expressed by Pfeffer (1897), Schimper (1898), Warming (1918) and others, and so strongly condemned by Maximov (1929) and his associates, is to be rejected altogether. In their effort to bring evidence for the assumption that xerophytes possess a higher intensity of transpiration than mesophytes, Maximov and his associates used a series of plants not critically chosen as xerophytes. Among other plants that Maximov considered as xerophytes were the exceedingly deep rooting *Alhagi* and *Haloxylon ammodendron*, the clearly mesophytic *Portulaca* and *Zygophyllum fabago*, etc.

Our examinations clearly show that plants growing under extreme drought not only show a very low transpiration intensity as compared with the less xerophytic Mediterranean plants but also use pheno-ecological and pheno-morphological properties for further reduction of water loss. This is far from agreeing with the view of Maximov on xerophytes.

Not less contradictory to Maximov's view is the fact that among the permanent desert vegetation not a single plant has been found 'with a capacity of enduring wilting without injury', a character so strongly assigned by Maximov to xerophytes. What is very striking in desert plant life is that plants of the permanent vegetation are physiologically active the whole year round; some of them flower just at the end of the dry season, some set fruits. None of them are so-called 'stop and wait' plants.

The present study may thus supply substantial data for the reconsideration of some aspects of the older view on the water ecology of desert plants. Where the habitat is exposed to permanent or seasonal drought, the biseasonal vegetation is exceedingly thrifty in its water expenditure, both in the rainy and the dry season. This is well shown by the transpiration intensity values, in the phenological events of the plants falling in the 'right time', and in their morpho-ecological behaviour resulting in a considerable reduction of the transpiring body during the drought period. The permanent vegetation is active the whole year round.

In the permanent desert vegetation of the area concerned the following hydro-economical combined types may be distinguished:

(a) High transpiring, evergreen deep-rooters with transpiration increasing in summer (e.g. *Acacia* spp.).

(b) High transpiring, evergreen deep-rooters with transpiration decreasing in summer (e.g. *Tamarix* spp.).

(c) Low transpiring, biseasonal and surface reducing deep-rooters with transpiration increasing in summer (e.g. *Atriplex halimus*).

(d) Low and medium transpiring, biseasonal and surface reducing spartoid deep-rooters with transpiration decreasing in summer (e.g. *Retama* spp.).

(e) Low and medium transpiring biseasonal and surface reducing articulate deep-rooters with transpiration decreasing in summer (e.g. *Anabasis articulata, Haloxylon articulatum*).

(f) Low and medium transpiring, biseasonal, surface reducing, non-succulent flat-rooters with transpiration decreasing in summer (e.g. *Artemisia Herba alba*).

(g) Low and medium transpiring, biseasonal, surface reducing, glyco- and halo-succulent flat-rooters with transpiration decreasing in summer (e.g. *Zygophyllum dumosum, Reaumuria palaestina*).

Summary

(1) The Near East deserts constitute a more or less uniform entity in its climatical and vegetational aspect but is heterogeneous from the point of view of plant hydro-ecology.

(2) As moisture is the minimum factor, all features associated with hydro-ecology are of supreme importance to plant life.

(3) There is a variety of morphological, phenological and physiological types among the local vegetation, all reducing the amount of water expenditure lost through transpiration.

(4) Of the various life forms the chamaephyte biseasonal are the most important elements in the evergreen vegetation cover of the desert.

(5) The life form analysis in its conventional approach is of little significance to hydro-ecology. But in the light of seasonal surface reduction of the transpiring body it is hydro-ecologically very important.

(6) A variety of morpho-ecological types has been distinguished among the permanent vegetation of the desert. In most of them seasonal surface reduction is considerable.

(7) Both with regard to transpiration intensity and to osmotic pressure of cell sap, various types have been distinguished in the vegetation of the desert.

(8) An attempt has been made to establish combined hydro-economical types based on properties, associated with the water-economy of the plants.

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THE OCCURRENCE OF PLANT DISEASES IN ARID CLIMATES AND THEIR AGRICULTURAL SIGNIFICANCE

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INTRODUCTION

One of the great advances in plant pathology in the last thirty years is without doubt the recognition of the responsibility of environmental factors in the occurrence and distribution of plant diseases. The significance of these factors and especially of climate, has been appreciated for a long time by plant growers, who take them into consideration whenever plant introductions are made. Unfortunately, however, the phytopathological side is still much neglected. The fact that plant diseases can be introduced along with plants has not always been given the consideration that it deserves.

In another place (Reichert, 1950), I described phytopathogeographical methods that enable plant growers to be more certain in predicting the reappearance of plant diseases that may have been introduced with their hosts.

The application of these methods makes possible the exact planning of new importations and may obviate diseases otherwise incurred by introducing plants from foreign places.

It will be shown that the exothermic climate may be utilized within the frame of phytopathogeographical planning for plant disease - control. The application of the principles to be described will diminish to a great extent the affliction of crops by diseases. It is known, that only a limited number of pathogens are able to establish themselves and achieve their cycle of development in a xerothermic climate. This key fact must therefore be utilized whenever introductions are made and the timing of seasonal cultivations planned. The most important point that must be kept in mind in respect to xerothermic climates is that a great part of the summer (the chief growing season for many crops) is either rainless or nearly so, and that only a relatively few pathogens can surmount this obstacle and accomplish their cycle of development. This fact has great agricultural significance.

Below, some examples taken from observations on plant diseases made in Israel and other parts of the Middle East are quoted. The maladies mentioned are hampered in their development in this area which is characterized by rainless summers, and a winter precipitation (from November – December to March – April). In Israel this diminishes in quantity from North to South and from West to East, thus, Safad in the mountains of northern Galilee has an average of 744 mm. of rain per year, whereas Beersheba in the South (Negev) has 193 mm. and Haifa on the coast has 612 mm. There is approximately 400 mm. average yearly rain in Ain Harod in the great interior valley of Jezreel in the eastern part of the country average July temperatures range from 22.4°C at Safad, 24.5°C at Beersheba, 25.5°C at Haifa, to 27.7°C at Ain Harod. Relative humidities during July average 48% at Safad, 65% at Beersheba, 74% at Haifa and 56% at Ain Harod. (Anon., 1938; Ashbel, 1949).

Cereals

Wheat. As the first example of a disease derived from a cool climate that sel-finds adequate conditions for development in arid climates, we may mention *Tilletia tritici.* It does not often occur in Israel, is especially rare in the interior valleys and is to be found only when rain and ensuing cold weather follow closely upon the sowing of the grain. The optimum temperature for seed germination is 25°C while that for germination of the spores is 10 - 16°C. Since rain generally does not appear until some time after sowing, the seedling usually has enough time in which to evade attack. Such a case was observed in Palestine in 1924 (Reichert, 1928 a). The same conditions and results are known in other xerothermic countries, such as southern India, southern Russia, the Spokane Valley in Washington, and others (Heald, 1933; Walter, 1950).

A second example is *Claviceps purpurea,* which is favoured by 'abnormally wet seasons with reduced amount of sunshine' (Heald, 1933). Since arid regions are always dry during the blossoming period of wheat, no infection can take place here. Avizohar (1947) was able artificially to produce this disease in Israel only by increasing the humidity around the plant by artificial means. Similar environmental conditions prevail in the distribution of the disease in other countries. (Heald, 1933).

Maize. One of the healthiest summer crops grown in Israel is maize, the only diseases affecting the plant here being *Puccinia sorghi* and *Ustilago zeae.* They occur only near the sea or under irrigation; conditions that raise the humidity to such an extent that the pathogen can successfully attack the crop. This is particularly true in the case of the rust. It is interesting to note that, although all the maize varieties were originally derived from localities in the U.S. and were sown here without seed treatment, they did not reveal any of the serious diseases recorded in other maize-growing countries, e.g. *Diplodia zeae, Sclerospora macrospora,* and *Physoderma zeae-maydis.* These three diseases require abundant and frequent rains throughout the growing period of the corn crop, conditions not to be found in arid regions. They are therefore also excluded from the arid south-western part of the U.S. (Heald, 1933; Walker, 1950).

Wheat and maize in our country have not been affected by bacterial diseases like *Pseudomonas translucens* var. *undulosa* and *P. desolvens,* that cause great damage in other countries.

Vegetables

A good example of how an arid climate can preclude or limit the occurrence of an important vegetable disease is to be found in the case of 'black rot' of cruciferous plants (*Pseudomonas campestris*). It is widespread in coastal regions of Israel (Reichert, 1939 b), but its presence in the interior valleys is limited to early spring and late autumn. In the U.S. a similar state of affairs exists, with the disease prevalent only in the humid areas east of the Mississippi. It is very rare in the Rocky Mountains and Pacific coast (Heald, 1933). Walker (1950) tells us that it is entirely excluded

from 'regions where the rainfall is very low during the period when seedlings are being grown'. According to him, 'black rot' is little known in the Puget Sound region in Washington and in Pacific coast areas where summer precipitation is low. In these regions, seed may be grown free from bacterial infection.

Solanaceous Crops. Characteristic, and of great agricultural import, is the mode of occurrence and distribution of some important diseases attacking potatoes and tomatoes in Israel. These crops are afflicted in warm, humid climates by three high-humidity-loving diseases, -*Pseudomonas solanacearum, Phytophthora infestans* and *Cladosporium fulvum.* In Israel they are to be found only in certain areas. *P. solanacearum* was found here only on potatoes and even then, only in the one year, 1947, in the coastal strip during a particularly damp spring and late autumn (Littauer, Volcani, & Temkin, 1926). *Phytophthora infestans* is considered in our country to be a serious menace to the winter-sown potatoes because of the abundant rain and the mild temperature that prevails in that season. But the opposite is the case in the late spring and the autumn, and the occurrence of the disease at this time is almost nil or very scarce in the interior valleys, in upper Galilee and in the dry Negev. It is interesting to note that until ten years ago, the disease was rather scarce even in the coastal region, but owing to the introduction of overhead sprinkling it has been on the increase. It seems to be a known fact in Israel that morning sprinkling is less conducive to disease than that carried out late in the day, as the latter method extends the time in which there is high humidity, and with it the possibility of infection. Even in the coastal belt, though, the disease is halted during the months of April and May by the drying sirocco winds (khamsin), and it renews its development in June.

Phytophthora infestans has been causing much damage to tomato crops within the last years, and we are paying a great toll to this plant invader. It makes incursions around the Sea of Galilee and in the coastal strip, but to a much lesser degree in the interior valleys and the Negev. In the late spring it does not appear at all in the Negev.

Cladosporium fulvum is a lover of high humidity (Walker, 1950) and therefore is limited to the spring and autumn in the coastal area and is not to be seen in the interior valleys.

Tomatoes are afflicted in our country and in many other Mediterranean countries by the xerophilic plant disease *Oidiopsis taurica,* which attacks them heavily in the interior valleys in the autumn, when the optimum relative humidity for the germination of spores is less than 70% (Reichert, 1939b; 1949). Potatoes, in turn, are attacked by an *Oidium* fungus which shows even greater xerophilic tendencies. Leaves are attacked only in regions where humidity is lower than 50% (Reichert, 1949).

Plantations

Deciduous trees. *Taphrina deformans* is a serious malady of stone-fruit trees in cooler countries. It appears in Israel chiefly on almond trees at higher altitudes in early spring, since almond is an early bloomer. It occurs also to a lesser extent on peaches. (Reichert, 1939c).

Another important disease of prunaceous trees in cooler climes is the 'scab' of apple and pear (*Fusicladium dentriticum* and *F. pyrinum*). Only the local varieties of these fruit trees, the early bloomers, fall prey to this malady, as they flower at a time when rain and high humidity are frequent. European varieties, which form blossoms and leaves three to six weeks later, when rain has already ceased and temperature gone up, escape the disease (Pelberger, 1944).

Very interesting is the occurrence of 'rust' (*Puccinia pruno-spinosae*) on prunaceous trees, especially almond. Whereas it is very serious in humid climates and even in the California coastal regions (Goldsworthy & Smith, 1931) due to the frequent fogs, it makes its appearance in Israel in June, after the cessation of the 'khamsin' wind season. In the interior valleys it is non-existant (Perlberger, 1943).

Another important disease of stone-fruits is 'brown rot' (*Monilinia fruticola*) This species is a menace to fruit cultivation in cool, humid countries (Heald, 1933; Walker, 1950), but does not appear in Israel, even under irrigation, for low soil moisture and air humidity, combined with the high temperature, of the summer, impede the attack upon the fruit blossoms.

Mediterranean trees. An interesting illustration of the controlling effect of xerothermic climate upon plant disease is provided by the diseases of some Mediterranean trees. First among these is the downy mildew of grapevine (*Plasmopara viticola*) which occurs in Israel only in the coastal region, and is checked in the interior valleys and in the higher altitudes of the Jerusalem area and the upper Galilee (Reichert, 1927). In valleys the appearance of the disease is hampered by the high prevailing temperature, amounting to 29-29.9°C during the growing season, which is the maximal germinating temperature of the conidia of the pathogen. In elevated localities, on the other hand, the lower relative humidity and the scarcity of dew through wind action precludes the occurrence of the disease (Reichert, 1927).

It might be worth mentioning that another important disease of the vine, *anthracnose* (*Gloeosporium ampelophagum*) does not occur at all in Israel and neighbouring countries. The reason for its absence here lies in its tropical origin; it is prevalent in the warm, humid climates, of the low-latitude Atlantic countries of Eurafrica, the Western Caucasus, south-eastern North America and parts of the southern hemisphere. It may be of interest to mention the fact that wine growers in our country had treated vines against this disease for more than thirty years, having been influenced by French instructors to whom the disease was a common thing. We were able to convince them that the treatment was unnecessary, since the disease is non-existent here.

Another serious vine disease of cooler countries that does not occur in Israel and the rest of the eastern Mediterranean area, nor in the arid parts of the U.S. and other countries, is *Botrytis cinerea.* The high humidities required by this pathogen are not present in these countries during the summer.

A characteristic disease of olives, *Cycloconium oleaginum,* which causes leaf-drop, is to be found here chiefly in the coastal region since the interior valleys and Galilee have not the high humidity that the parasite demands. When olive trees are irrigated however, the disease becomes evident to a small extent even there.

In 1934, when visiting the vast plantations of *Pistatia vera* in the great steppes east of Aleppo, we noticed that the trees were completely free of any disease, whereas westward towards the seaport of Lattaquieh, we found them heavily infected by *Septoria pistaciae*.

Citrus trees. The limiting effect of dry weather conditions upon plant disease is particularly pronounced in the case of citrus diseases, and is evident in Israel and adjacent countries. The arid conditions of this region exclude two diseases that in warm humid countries are considered to be among the worst scourges of citrus. They are 'scab', caused by the fungus *Sphaceloma fawcetti*, a near relative of the anthracnose of vine, and 'canker', a bacterial disease caused by *Phytomonas citri* (Fawcett, 1936). Peltier & Frederick (1922) revealed the dependence upon warm and very humid conditions of these diseases.

Another bacterial disease, *Phytomonas syringae*, the causative agent of 'blast' of of citrus, develops in our country only when the autumn is particularly rainy and cool (Reichert & Perlberger, 1928; Reichert, 1939b).

Industrial Plants

Tobacco. Although this country has for many years been importing tobacco seeds from U.S.A. and other countries that grow the crop under warm, humid conditions, there has been no emergence of the very serious diseases that tobacco has been heir to in the countries whence the seed came; we have not found to date any of the downy mildews such as *Phytophthora nicotiana*, *Peronospora hyoscyamae*, nor the various bacterial diseases that affect tobacco. Even *Bacterium solanacearum*, which was mentioned above as having once attacked potatoes in the spring here, has failed to appear on tobacco in Israel. The reason is that the crop here is grown during the dry summer.

Other instances of summer crops avoiding fungal attacks are provided by the sunflower (*Helianthus annuus*) and safflower (*Carthamus tinctoria*), both of which, in cool damp countries are prey to *Sclerotinia sclerotiorum*. Safflower is attacked also by a downy mildew, *Plasmopara halsteadii*. In Israel these diseases make no headway whatever in the summertime, the optimal temperature for the germination of the ascospores of *Sclerotinia sclerotiorum* being 17°C: much lower than the average prevailing temperature of the air during the growing period of the host. Besides, the parasite demands a great amount of soil moisture for the fruiting bodies to discharge their spores.

DISCUSSION

The accumulated data regarding crop plants escaping disease when grown in hot, arid, regions show clearly how important these regions, including steppe and desert may become for agriculture. All these vast, neglected lands, hitherto considered as 'barren', may be transformed into productive, remunerative agricultural areas for growing crop plants since these are here less subject to the attacks of dangerous parasites than if they are grown in humid areas. Thus free of such troubles, the grower is able to devote his energies to the control of the few xerophilic diseases remaining. For instance, great areas of vineyards in the interior valleys of Israel, in the neigh-

bourhood of Damascus and in lower Egypt remain untouched by the standard maladies that are usually met with in humid regions. The only serious disease remaining here is powdery mildew, and this can be easily controlled. Citrus and other southern trees escape the bulk of plant plagues if grown in xerothermic regions. This is especially true of the leaf diseases usually concomitant with them in warm, damp climates. Thus grapefruit groves in the interior valleys of Israel, as well as the large citrus plantations in the vast western desert of Egypt are free from all leaf diseases. The same may be said of cereals, particularly maize, and of many vegetables and industrial plants, all of which, under these conditions, are quite free of hygrophilic diseases.

The above data show that, a distinction must be drawn between two types of xerothermic region. The first may be designated as interior areas, far removed from the sea, which are characteristically free of certain diseases. The second type comprises the area bordering the sea. It is naturally subjected to higher humidity and to humid breezes, which modify the immunity found in the areas of the first category. For example, the downy mildew of vine (*Plasmopara viticola*) which is prevalent, in a mild form in the coastal plains of the Mediterranean, disappears in steppes and deserts far from the coast (Reichert, 1927).

Another important factor in the controlling effect of arid climate on plant disease must be recognised. This, is the difference between summer and winter periods. The winter climate in a xerothermic region is cooler and more humid than that of summer, and therefore may enhance the development of certain diseases that are suppressed in the summer. Thus, *Sclerotinia sclerotiorum* attacks plants during the winter and not during the summer because it has a low minimal temperature – 1°C and a low optimal temperature – between 17 and 21°C. Decisive factors in the success of infection are the amount of precipitation, the relative air humidity, dew, and last but not least, the altitude of the locality.

As a good example, the distribution of the vine disease, *Plasmopara viticola* may again be mentioned. This is limited to the coastal plains where sufficient humidity and dew are present, whereas it disappears in the inland valleys where they are absent, as in the high mountains of Galilee, where freely blowing winds quickly dry up any dew that is formed and diminish humidity of the air. The great importance of humidity in arid countries in the propagation of the *Plasmopara* pathogen was demonstrated during this study of the comparative distribution of the disease (Reichert, 1927).

Another important ecological point that must be emphasized is the duration of night and the subsequent dew formation. In northern countries, parasitic fungi avail themselves of the necessary dampness for infection both in the night and in the daytime. In the dry regions however, these conditions prevail only during the night. It has been demonstrated experimentally by a study of the ecological conditions on downy mildew of cucumber (*Pseudoperonospora cubensis*) the extent to which dew formation is essential for the development of diseases in dry regions. When dew was prevented from forming on plants by means of canvas covers, no infection took place (Goldsworthy & Smith, 1931).

The change from furrow irrigation to overhead sprinkling must also be considered if one is to obtain a clear picture of the value of arid region farming. The general belief in Israel is that the rapid spread of late blight (*Phytophthora infestans*) is due to the abandoning of the old furrow method for the intensive use of overhead sprinkling. In the case of the cucumber disease already mentioned, this has been experimentally established. (Duvdevani, Reichert & Palti, 1946). Sprinkling changes the microclimate of the plants by increasing the moisture on the leaf surface and the moisture over a greater area of soil. Consequently a greater opportunity for parasitic activity presents itself.

It is noteworthy that in arid regions, root and stem diseases are more prevalent than leaf diseases, and may also appear in irrigated crops, but never to the extent found in humid areas.

In xerothermic climate there are, therefore, two primary components which operate in the inhibition of plant diseases – high temperature and low humidity. The relative importance of each factor depends upon the origin of the disease. With those derived from a cooler climate, as *Tilletia tritici, Sclerotinia sclerotiorum, Phytophthora infestans,* etc. the high temperature is the limiting factor, but in the case of pathogens originating from tropical countries, such as *Bacterium colanacearum,* scab of citrus (*Sphaceloma fawcetti*), and citrus canker (*Phytomonas citri*), the low air humidity becomes decisive in the inhibition of the diseases.

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PHYTOSOCIOLOGIE ET MISE EN VALEUR DES SOLS EN AFRIQUE DU NORD

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L'Afrique du Nord Française à l'intérieur de ses limites politiques est au 9/10° aride ou semi-aride.

Les travaux que nous y avons entrepris sont nés des préoccupations des Gouvernements de nourrir une population qui s'accroît régulièrement tous les ans.

Le problème est, en effet, urgent: l'accroissement de la population est tel qu'il faut tous les ans un supplément de 50,000 tonnes de céréales, chiffre basé sur une ration de 300 gr. par jour.

Il est donc nécessaire de trouver des terres.

L'aspect humain du problème n'est pas le seul, on comprend qu'il ait aussi un côté politique.

Les trois gouvernements de l'Afrique du Nord ont décidé la mise en valeur des périmètres suivants:

En Tunisie:	Vallée de la Medjerda, Tunisie centrale (pays de Sbeitla, Kasserine, Cap Bon, littoral septentrional, Oasis du Sud.
En Algérie:	Vallée du Chélif, région de Bône, Sahel d'Alger, environs d'Oran, Hauts-Plateaux, confins algero-marocains méridionaux.
Au Maroc:	Tadla-Beni Amir (pied occidental du Moyen Atlas méridional), Haouz – pays d'El Kelâa, Doukkala (sublittoral), Gharb, pays de Berkane (Maroc oriental)

Toutes ces régions sont arides ou semi-arides.

Comment le phytosociologue peut-il contribuer à la mise en valeur rationnelle du sol?

On sait que, dans la nature les espèces ne sont pas réparties sans ordre et d'une manière quelconque, mais qu'elles constituent des *groupements* ordonnés, hiérarchisés, floristiquement définis, que nous appelons *associations*.

Or, la grande valeur pratique de cette notion est qu'à l'intérieur d'un même territoire floristique, la même association se retrouve chaque fois que les conditions écologiques sont les mêmes. A chaque association correspond une écologie déterminée.

Sur toute l'étendue d'une association les conditions écologiques sont les mêmes.

Il y a correspondance entre associations et milieux, d'une part, entre milieu et vocation, d'autre part, donc, aussi entre associations et vocations.

Etant donné cette solidarité, nous pouvons établir une *carte* des milieux, si nous cartographions les associations.

Nous avons ainsi entrepris, en Afrique du Nord, sur une grande échelle, des travaux de *cartographie des associations*.

Ces cartes sont donc, en fait, des cartes de *vocation des sols*. Elles sont établies au 20,000°, parfois à des échelles plus grandes encore suivant les besoins.

Mais, dira-t-on, comment *pratiquement*, ces cartes des associations peuvent-elles nous indiquer quelles sont les aptitudes agronomiques des sols qui les portent?

Nous procédons comme les géologues. Ceux-ci savent, par example, dans quelles conditions tectoniques on troube le pétrole. Ils dressent donc la carte géologique et font des forages là où les structures correspondent à celles qui ont été observées.

Ainsi, nous étudions avec soin, en plus des associations, les essais de cultures, réussis ou non, faits dans le périmètre dont nous levons la carte phytosociologique. Si une culture a donné de bons résultats dans une association, il est clair que les mêmes résultats peuvent être obtenus partout où la dite association existe.

En Tunisie méridionale, par exemple, l'une des questions posées était de savoir jusqu'où il était possible d'étendre les oasis existantes, mais devenues insuffisantes pour la population.

Le problème a été résolu par la méthode phytosociologique. Nous avons constaté que les Palmeraies étudiées étaient installées empiriquement par les Indigènes dans des associations déterminées. (Assoc. à *Suaeda fruticosa* et *Salsola tetrandra*, Assoc. à *Limoniastrum guyonianum* et *Halocnemum strobilaceum* (sous-assoc. à *Arthrocnemum*)). En cartographiant ces associations favorables au Dattier, nous avons pu définit les limites d'extension possible et déterminer des régions ou de nouvelles palmeraies pourraient être créés, pourvu que l'eau nécessaire soit disponible.

Si aucune expérience n'a encore été faite, soit dans une région donnée ou avec une plante exotique intéressante que l'on voudrait introduire, la méthode est un peu plus compliquée. On fera des essais dans les régions à climat susceptible de convenir a priori à la culture, comparable à celui du pays d'origine de l'espèce envisagée. Mais on fera les essais *dans des associations déterminées*. Les résultats indiqueront quelles sont les associations indigènes les plus favorables à la culture projetée.

L'expérience agricole préalable n'est même pas toujours nécessaire. Nous savons, par exemple, que la plupart des cultures de plantes annuelles (blé, etc. ,) ne peu vent être faites immédiatement dans certaines associations (Assoc. à *Lithospermum fruticosum*, à *Erica multiflora*, etc. ,). Le sol de ces associations est intoxiqué par les sécrétions des racines des principales espéces qui la constituent. On peut cultiver dans de tels sols, en fait d'annuelles, que des Légumineuses, dont les nodosités contiennent des antitoxiques; pour les autres cultures annuelles, il est nécessaire d'attendre jusqu'à ce que les pluies aient suffisamment lavé les sols qui ont été habités par les associations toxiques.

Un autre exemple nous a été donné par un grand domaine de Tunisie centrale. Cette propriété a été plantée d'Oliviers, d'Amandiers et d'Abricotiers, dans un sol qui paraissait parfaitement homogène. Or, au bout de 10 ans, les arbres ont décliné dans une partie de la propriété, tandis qu'ils continuaient à vivre normalement sur le reste du domaine. Nous avons procédé à une étude phytosociologique et constaté que la propriété était établie dans *une* association, mais que sur certaines parcelles, cette association existait sous forme d'un *faciès* caractérisée par la présence très dispersée d'une Salsolacée (*Salsola tetrandra*). Or, ce faciès indique qu'il y a du sel à *plusieurs mètres* de profondeur. Les arbres fruitiers, au début de leur plantation, ont donc pros-

péré normalement, mais au bout de 10 ans tous ceux qui étaient dans le faciès à *Salsola,* leur racines touchant le sel, ont dépéri. Si un phytosociologue avait prospecté le domaine *avant* laplantation, il aurait pu délimiter avec précision les parcelles favorables à l'arboriculture et celles où seules des cultures herbacées, à enracinement faible, étaient seules possibles.

Et le sol dira-t-on? La connaissance du sol est naturellement capitale aussi, car il n'y a pas d'étude phytosociologique complète sans fiche pédologique, mais notre expérience nous permet de donner un avis formel sur un point: La prospection phytosociologique doit *précéder* les recherches pédologiques. Etant donné qu'il y a correspondance étroite entre les associations et la pédologie, les pédologues peuvent gagner beaucoup de temps en prélevant les profils *par associations,* non *par unité de surface* à prospecter. Un seul profil peut suffire pour toute la surface, même très grande, si celle-ci n'est occupée que par une seule association.

Inversement, la diversité phytosociologique doit inciter les pédologues à multiplier les trous là où ils seraient tentés de n'en faire qu'un petit nombre, s'ils n'étaient pas guidés par la phytosociologie. Dans la vallée de la basse Medjerda (Tunisie), les pédologues ont pu utilement diriger leurs prospections en tenant compte des groupements végétaux, certains sols leur ayant échappé avant qu'ils eussent connaissance de ces faits.

La méthode exposée ici est générale, applicable à tous les cas, bien entendu aussi à tous les pays arides ou semi-arides.

J'ai l'honneur de vous présenter deux cartes, l'une d'Algérie (Basse vallée du Chélif), l'autre de Tunisie centrale établies par mes collaborateurs pour les Gouvernement respectifs.

Je commenterai brièvement la carte Tunisienne.

Elle est couverte par 27 Associations définies suivant la méthode pratiquée à MONTPELLIER. Les vocations économiques des surfaces couvertes par les associations sont très diverses; en voici quelques exemples:

Les associations à *Rosmarinus officinalis – Stipa tenacissima – Reseda papillosa* et celle à *Launaea mucronata – Erodium glaucophyllum* ont une vocation forestière (*Juniperus phoenica, Pinus halepensis*), mais la forêt sera plus difficile à installer dans la 2° association que dans la première.

L'Association à *Eragrostis papposa – Ziziphus Lotus - Artemisia campestris* et à *Chrysanthemum coronarium – Peganum harnala* sont excellentes pour l'arboriculture fruitière (Amandiers, Oliviers, Abricotiers).

Une sous-association (à *Stipa parviflora*) de l'association à *Eragrostis* forme d'excellents pâturages.

L'Association à *Aristida pungens* et *Rumex tingitanus* var. *lacerus* convient à des plantations d'*Opuntia.*

L'Association à *Artemisia herba alba – Haloxylon tamarises folium* (sous-association de *Stipa parviflora*), en mélange avec l'association à *Plantage lagopus – Silybum eburneum* est apte aux Céréales.

Dans l'association à *Salsola vermiculata* var. *villosa* on peut encore planter des Figuiers et des Amandiers, et des culture de céréales sont possibles; elle n'est pas trop salée. Mais les surfaces couvertes par l'association à *Limoniastrum - Salsola cruciata,* souvent en contact avec la précédente, sont à éviter soigneusement. Ces 2 associations, surtout la première, peuvent être utilisées aussi comme pâturages.

Certains groupements, tels que l'association à *Arthrocnemum glaucum* et celle à *Halocnemum strobilaceum* sont impropres à toute mise en valeur, en l'état actuel de la situation bien entendu.

LES RELATIONS ENTRE LES ZONES DÉSERTIQUES ET LA PULLULATION DES PARASITES DES PLANTES

Professor Paul Vayssière

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A ma connaissance, la pullulation des parasites des plantes, cultivées ou spontanées, dans ses rapports avec les conditions créées par les déserts et les sub-déserts, n'a encore jamais fait l'objet d'observations d'ensemble d'autant plus que, suivant l'espèce des êtres considérés et suivant la spécialité du biologiste intéressé. Le rôle joué par les zones arides et semi-arides peut être opposé et, en tout cas, différent.

Malgré, la complexité du problème, je vais m'efforcer, par quelques exemples frappants, choisis dans des groupes aussi éloignés que possible, de mettre en évidence son aspect double et contraire. Toutefois, il me parait impossible, dans ce simple exposé, de séparer les régions typiquement désertiques – déjà si différentes entre elles – des zones qui les entourent et qui ne sont qu'à demi arides. Là, l'Homme, grâce à sa ténacité et parfois à son génie, a pu installer des cultures qui constituent des ilôts encerclés d'aires couvertes d'une végétation xérophile plus ou moins spontanée, laquelle favorise la pullulation d'animaux phytophages susceptibles de jouer, un jour ou l'autre, un rôle économique non négligeable. Pour étayer son action l'Agronome doit donc tenir compte des êtres vivants qui évoluent et se multiplient dans ces régions sub-désertiques, steppes ou savanes a écologie si complexe sous la dépendance des facteurs climatiques, et surtout microclimatiques en ce qui concerne les parasites des végétaux.

Dans de nombreux cas, les surfaces arides, par les conditions mêmes qui les caractérisent, constituent des barrières infranchissables pour les parasites des plantes, que celles-ci soient spontanées ou cultivées. Mais les moyens de transport de plus en plus perfectionnés et rapides mis à la disposition de l'Homme ont supprimé cette protection naturelle de sorte que de tels parasites ont progressé lentement d'oasis en oasis, le long des pistes avec les caravanes, tandis que d'autres se trouvaient transportés par des voies plus rapides. Deux exemples pour illustrer cette assertion: il est incontestable que le Ver rose de la capsule du Cotonnier, le Pink Bollworm (*Platyedra gossypiella* Saund.) qui était signalé en Egypte dès avant 1910, n'a jamais pu, par ses propres moyens, traverser les régions sahariennes pour se répandre dans les cultures cotonnières de l'Afrique occidentale bien que le genre *Gossypium* existe dans la plupart des oasis. Il a fallu des envois, plus ou moins clandestins, par poste ordinaire ou par la voie des airs, en Nigeria et en Afrique française, de semences égyptiennes sélectionnées, pour que ce dangereux parasite puisse s'implanter dans les cultures au sud et a l'ouest du Sahara. Les cochenilles spécifiques du Dattier (*Phoenix dactilifera*) telles que *Phoenicococcus marlatti* Ckll. et *Parlatoria blanchardi* Targ. ont, elles, progressé lentement. De fortes présomptions situent leur pays d'origine dans le Moyen-Orient, peut-etre dans la région de Sinai (oasis d'El Arish) où Bodenheimer les a

étudiées (1924) sur des palmiers qui ne souffraient pas de leur présence, malgré une une grande abondance d'individus; par le déplacement des caravanes, elles ont peu à peu étendu leur aire d'habitat vers l'ouest du continent africain si bien que, à l'heure actuelle, celle-ci se confond avec celle du Dattier? Les diverses étapes de cette extension ont été notées successivement, sur le territoire saharien francais, par L. Trabut, P. Vayssière, A. Balachowsky.

En ce qui concerne les parasites végétaux, nous n'avons que très peu d'observations précises sur le rôle utile joué par les déserts vis-à-vis des plantes cultivées en particulier. Toutefois, il y a lieu de rappeler que, pour un grand nombre d'espèces de Cryptogames, les conditions des zones désertiques altèrent leur pouvoir de germination, donc de propagation. C'est ainsi que *Puccinia graminis* remonte bien la vallée du Nil jusqu'a 60 km. environ au sud d'Assouan (observation personnelle de M. Viennot-Bourgin en 1936) mais est incapable de parasiter les Céréales et les Graminées sauvages au-delà de ce point par manque d'humidité. On ne le rencontre donc pas au Soudan anglo-égyptien.

A côté du rôle utile que peuvent jouer les zones arides – rôle altéré par les transports: ce qui le fait de l'Homme – il en existe un autre, néfaste et particulièrement important, surtout pour les zones semi-arides: c'est qu'elles peuvent servir de refuge, et en conséquence de zones de multiplication, pour certains animaux et végétaux. Que ce soit pour répondre aux nécessités de l'espèce ou pour suivre les lois de l'expansion, il arrive toujours un moment où ces êtres vivants se répandent sur les régions avoisinantes, et même parfois lointaines et deviennent, très souvent, de véritables fléaux. On peut alors voir des espèces phytophages, typiques ou occasionnelles, qui s'abattent sur les cultures et les détruisent rapidement, ou s'adaptent à elles et les anéantissent progressivement, réduisant fréquemment à la misère les populations de régions déjà défavorisées. De nombreux exemples peuvent être fournis et le plus marquant, comme le plus connu, est celui des Acridiens migrateurs, ou tout au moins de certaines espèces d'entre eux. Le plus caractéristique est, évidemment, le Criquet pélerin (*Schistocerca gregaria* Forsk.) dont les aires de multiplication (aires grégarigènes) se localisent, en Asie et en Afrique, en bordure des immensités désertiques nord-équatoriales de l'Atlantique au Pakistan et en Inde, en passant par l'Arabie et la Perse. Quant à *Locusta migratoria* s.l. ne peut-on placer, sans discussion possible, les principales aires grégarigènes dans des zones semi-désertiques?; estuaires des grands fleuves des bassins fermés en voie de disparition, en Russie méridionale et en Asie pour *Locusta migratoria migratoria,* ancien delta du Niger pour *Locusta migratoria migratorioides.* Dans le sud de Madagascar, les aires grégarigènes de *Locusta migratoria capito* se rencontrent dans une contrée aride, avec un sol léger, sablonneux exposé à être inondé par taches au cours des pluies; certains points favorables à la constitution des foyers grégarigènes sont sur latérites dures.

Un autre Acridien, non typiquement migrateur, mais incontestablement grégaire, *Anacridium moestum malanorhodon* Walk. joue lui aussi un rôle économique non négligeable en Afrique nord-équatoriale, dont il parait bien acquis (Morales, Roblot) que l'aire permanente se trouve dans le Sahel, et dans la zone côtière du Sahara espagnol. Cette espèce, sous certaines conditions, émigre parfois vers le sud.

D'autres Orthoptères, non grégaires, viennent également des zones désertiques ou semi-désertiques pour s'attaquer aux cultures. G. de Lotto (1951) a constate que, en Erythrée, *Pymateus viridipes* depose ses oeufs dans les sols, incultes, pierreux ou de sable compact; les larves, dont l'évolution dure environ 4 mois, restent dans les zones semi-arides et ne sont donc pas considérées comme nuisibles. Mais les adultes, les femelles en particulier, qui vivent 7 mois, se deplacent vers les cultures et défeuillent les Vignes, les Figuiers, les Céréales, etc.

Certains groupes d'Insectes, bien que phytophages, paraissent inféodés aux régions désertiques; tels sont, chez les Coccides, genres *Margarodes* et *Neomargarodes* par exemple. La plupart des espèces récoltées l'ont été dans des étendues arides où elles vivent pendant une partie de leur existence sur les racines des rares végétaux xérophiles. Au cours de leur évolution elles ont un ou plusieurs stades de resistance enkystés, bien connus sous le nom de perles de terre (ground-pearl) ou perles du désert. Leur adaptation à des plantes cultivées peut se produire dans certaines circonstances. Ce fut le cas du *Margarodes vitium* Giard au Chili et en Argentine. Cette cochenille, particulièrement remarquable, a attiré l'attention du jour où, vers 1890 ses attaques, très sérieuses, sur la Vigne furent constatées au Chili. Son origine fut alors recherchée et l'on constata qu'il s'agissait d'un insecte polyphage précédemment observé dans des vallées incultes, loin de toute Vigne. Les kystes étaient fixés en grand nombre sur les racines d'un arbrisseau du genre Baccharis qui porte vulgairement le nom de "chirca" (Valery Mayet) (probablement *Baccharis spinosa*). Ce végétal est un des rares qui se rencontrent en lisière de la pampa d'Atacama où, actuellement, des periodes de 20 à 30 ans peuvent s'écouler sans que tombe la moindre averse!

Bien d'autres insectes phytophages trouvent dans les régions désertiques des conditions favorables à leur pullulation: *Kawiria Gabrieli* Schüst., *Tenebrionide Platyopinae,* sur le Saxaoul (Reymond) dans le désert de Kawir (Perse), *Foleya brevicornis* Peyer, *Tenebrionide Erodiidae,* qui fut récolté par myriades dans l'Erg occidental (Sahara) par A. Reymond, sur les epis de Drinn (Aristida pungens) en février - avril 1946 et 1947. Il y a aussi une foule de Bostrychides, de Scolytides, de Buprestides, qui passent de végétaux indifférents a des plantes cultivées ou seulement exploitées. Un Cérambycide, *Polyarthron pectinicornis* Fairm. pullule dans les oasis sahariennes, en août et septembre, aux dépens du Dattier. Enfin, une mention spéciale doit être faite des Scarabéides: *Rhizotrogus, Annoxia, Phyllopertha, Polyphylla,* dont les larves trouvent un milieu permanent très favorable à leur dévelopement dans les steppes circum-désertiques, et qui, sporadiquement, commettent des déprédations très sérieuses dans les plantations souvent très éloignées. C'est le cas de *Polyphylla fulla* qui, au Maroc, ravagent les jeunes Cèdres en coupant les racines (A. Reymond *in litt.*).

Des exemples comparables peuvent être fournis pour des animaux supérieurs et H. Heim de Balsac a bien voulu m'en fournir qui intéressent essentiellement les régions sahariennes: alors qu'en Europe le grand Corbeau, *Corvus corax,* fuit l'Homme, aux approches du Sahara, au contraire, il s'y est complètement inféodé et la densité de l'espèce y est même fonction de l'importance de l'agglomération. Le vicariant désertique, *Corvus ruficollis,* se comporte de même. Il s'installe à proxi-

mité des campements, perchant sur les Chameaux et dévorant les Tiques fixées sur les parties génitales. Tous ces Corbeaux, de quelque espèce qu'ils soient, sont de grands destructeurs de Céréales et de Dattes.

En Afrique du Nord, les cultures de Céréales ont encore à souffrir des incursions massives des Alaudidés, tant sédentaires que migrateurs, et des Moineaux. Ces derniers peuvent devenir un fléau pour les cultures: Le Maroc est particulièrement alarmé par leurs bandes (plus spécialement de *Passer hispaniolensis*) qui deviennent migratrices ou erratiques et se répandent jusqu'au Sahara septentrional. A Atar, le Moineau désertique, *P. simplex* et le Bengali, *Oedemosyne cantaux*, s'attaquent aux épis immatures de Mil, à tel point qu'il est nécessaire d'entourer ceux-ci de chiffons pour les préserver.

Parmi les Mammifères il faut citer les Gerbillinés, les Mériones qui, attirés par les cultures, deviennent, dans le sud-ouest marocain, commensales des habitations et s'attaquent aux récoltes sur pied et engrangées et, même, aux excréments humains. Les arganeraies ont à souffrir de l'Ecureuil *Atlantocerus* qui consomme les fruits. Enfin, les Gazelles, Mouflons, Sangliers, causent des dégâts importants aux jeunes plantations d'*Opuntia inermis* que l'on essaie de multiplier dans l'Anti-Atlas et le pays Fekna. La plante est utile par ses fruits, mais les animaux sont très friands des raquettes qui constituent une réserve d'eau.

Ce qu'il importe de souligner, en regard de tous ces exemples qui pourraient, aux espèces près, être valables sous toutes les latitudes, c'est que, nés dans des régions où les conditions de vie sont particulièrement inclémentes, ces animaux semblent en être devenus plus agressifs, donc plus nuisibles, vis-à-vis des plantes cultivées et des denrées qui sont elles-mêmes à la base de la vie humaine.

Malgré la brièveté de cet exposé, j'espère avoir réussi, à faire ressortir, l'influence, double et contradictoire, des déserts et semi-déserts sur les pullulations nuisibles aux productions dont l'Homme tire sa subsistance. Mais il est un autre aspect du problème qu'il me semble impossible de passer sous silence: je veux parler de l'action de l'Homme lui-même dans la formation de ces zones arides et semi-arides.

Ici ce n'est plus l'aridité qui agit sur le comportement de l'Etre vivant, tout au moins dans le sens direct qui nous occupe, mais c'est ce dernier, au contraire, qui pèse sur les possibilités du sol jusqu'à, parfois, créer le désert.

En effet, n'est-il pas normal pour les nomades et leurs bêtes, dans les régions désertiques et semi-désertiques, de séjourner autour des points d'eau généralement entourés d'un végétation plus ou moins verdoyante? Il en résulte un piétinement et un pacage abusifs qui concourent à la disparition rapide de la couche végétale et à l'installation d'une zone sablonneuse et stérile s'étendant peu à peu au large du point d'eau jusqu'à suppression complète de toute végétation et impossibilité d'utiliser l'abreuvoir. Kachkarov et Korovine (Monod, 1942) citent l'exemple de l'Arizona où l'on a constaté l'influence considérable du pâturage excessif sur la stérilisation du sol: des espaces immenses couverts de Graminées et constituant des pâturages magnifiques ont été transformés en fourrés de Cactus, d'Agaves et d'autres plantes épineuses inutilisables par le bétail: un broutage exagéré qui a

provoqué la disparition progressive de la couverture herbacée primitive devenue incapable d'éliminer la végétation non comestible qui, finalement, l'a remplacée.

L'action néfaste de l'Homme s'exerca encore de bien d'autres manières: débasement, feux de brousse, cultures intensives, etc. qui épuisent le sol et favorisent l'érosion. Mais c'est là une face du vaste problème des zones arides et semi-arides qui sort du cadre de cet exposé. Je voulais seulement faire ressortir que, s'il ne peut empêcher certaines conséquences de l'existence actuelle de régions désertiques, l'Homme a non seulement le devoir de lutter contre ces conséquences mais, avant tout la responsabilité de ne pas concourir à en créer de nouvelles. De plus, il lui incombe, tout d'abord, de fertiliser ces terres, dites semi-arides, qui possèdent encore quelques possibilités d'alimenter une végétation, si maigre soit-elle, avant de porter ses efforts sur celles qui en sont incapables pour quelque raison que ce soit. Et une image me vient à l'esprit, qui est aussi un exemple: les Hollandais 'repoussent la mer' pied à pied donnant des terres a l'agriculture morceau par morceau, ne s'attaquant à une part nouvelle que lorsque la précédente com commence a répondre aux soins qui lui ont été portés... les déserts doivent etre vaincus de la meme manière, avec méthode et ténacité, avec aussi une grande patience!; alors certains fléaux des cultures – et je pense en particulier aux acridiens – ne trouveront plus les conditions qui favorisent leur pullulation, qui seule, nous importe au point de vue économique et, en conséquence, social.

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THE DESERT LOCUST AND ITS ENVIRONMENT

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The distribution area of the Desert Locust (*Schistocerca gregaria* Forsk.) coincides with that of the hot Palaearctic deserts, although its swarm migrations may temporarily extend beyond the limits of the latter, both southwards and northwards. From the broad biogeographical point of view, therefore, the Desert Locust can be regarded as a typical inhabitant of these deserts and it is of general interest to see to what an extent the biology of the species is adapted to the desert conditions and, in particular, whether such changes in the latter as may be induced by man, are likely to bring us nearer to a solution of the Desert Locust problem which has a reasonable claim to be regarded as the oldest problem of applied entomology.

The genus *Schistocerca* has a somewhat unusual geographical distribution, since it includes some 80 species of South and Central America, with a few penetrating to North America, while *S. gregaria* is the only species occurring in the eastern hemisphere. It is fairly closely related to a South American swarming species, but certainly quite distinct from it.

Another feature of the genus *Schistocerca* is that, as far as is known, its American members are arboreal in their habits, and this, again, makes *S. gregaria* an apparent exception and its partiality for deserts may suggest a great ecological and physiological divergence from its congeners. However, when speaking of deserts, one should bear in mind that perennial shrubs are an essential feature of many desert areas and, in particular, of some sandy tracts where even something approaching sparse woods can be found, where they have not been destroyed by man. Observations on the Desert Locust, particularly in the adult stage, indicate its tendency for sitting on shrubs or tall plants. This is particularly noticeable in swarms which normally roost for the night on shrubs and trees. In this respect, therefore, *S. gregaria* has retained the generic habit.

With regard to its food, while the Desert Locust feeds readily on a large variety of plants including grasses (Bhatia, 1940), the latter play only a minor part in its diet and the vast majority of its food-plants are either annual and perennial herbs, or shrubs. In this respect, the Desert Locust offers a sharp contrast to the Migratory Locust (*Locusta migratoria* L.) which is predominantly a grass feeder (Kozhanchikov, 1950).

We see, therefore, that, ecologically, the Desert Locust cannot be regarded as a typical insect of open desert, or of arid grasslands such as occur in the marginal desert areas. In fact, leaving aside for the moment the occurrence of swarms which extend well beyond ecological barriers, the species is normally not encountered everywhere in the desert regions, but mainly in certain areas such as well overgrown sand dunes on coastal plains, scrub belts along the beds of seasonal rivers and similar habitats which represent 'ecological islands' in the desert.

The physiological requirements of the Desert Locust do not suggest a high degree of adaptation to what is usually understood by desert conditions. The female locust lays eggs preferably in sand, but not in dry sand. Sand which is dry on the surface but moist underneath, is suitable. Other loose soils are also acceptable, provided they are moist. In the absence of moisture, eggs may be laid on the surface of the soil where they perish. A developing egg of the Desert Locust has very high humidity requirements, since it needs to absorb more than its own weight of water for successful development (Shulov, 1952). Therefore, the soil round the egg must preserve sufficient free moisture for some 12- 15 days of the incubation period.

When young locusts (hoppers) hatch, they must have sufficient green food, usually tender annual plants which rapidly spring up in sandy desert areas after a shower of rain. Excessive heat and dryness during the hopper development, which takes 5-6 weeks, has been known to cause wholesale mortality of hoppers.

Adult Desert Locust are known to be able to survive for many months in conditions of dryness, but for their sexual maturation they require either succulent green food or high air humidity (Hamilton, 1950; Norris, 1952); in this respect, desert conditions are definitely unfavourable for reproduction.

With regard to activity, it has been thought before that adult locusts, particularly in swarms, would be most active in intensely dry and hot conditions and this would cause them to migrate to more favourable habitats, but recent observations (Waloff, 1952) tend to dispel this idea, since flight activity of swarms appears to be more persistent at higher air humidities than at the lower.

It would appear, on the whole, that the Desert Locust is far from well adapted to general desert conditions, and the question arises how can the species not merely survive, but be able, from time to time, to multiply in fantastic numbers.

The answer is to be sought in the fact that the widespread conception of a desert is too generalised. It covers a great variety of landscapes, which provide desert animals with a wide range of habitats, some of them offering very favourable conditions of life. In addition to this variety of conditions in space, there is a great seasonable variation in all life conditions: a truly desert, lifeless area becomes covered by lush annual vegetation almost immediately after a shower of rain.

The existence of such favourable ecological islands is the essential condition for the existence of the Desert Locust. Since, however, many of such islands are only ephemeral, they are clearly unable to support a stationary locust population. On the other hand, an insect which is capable of moving from one favourable area to another, has an excellent chance of survival, and the continuous existence of *S. gregaria* in the desert regions is closely bound up with its migratory or, rather, nomadic habit.

Most biologists would be content to accept the beneficial value of migration as a sufficient explanation of the migratory pattern, but it is possible now to offer a somewhat deeper analysis of this phenomenon.

Studies of Desert Locust migrations in relation to weather factors (Waloff & Rainey, 1951; Waloff, 1952) have shown that swarm displacements are closely linked up with weather dynamics, and Rainey,(1951) put forward a well-documented hypothesis that

major swarm movements take place towards zones of convergence of air-masses which are often associated with precipitation. The result is that locusts and rain are likely to arrive in an area together, an occurrence which has been frequently noticed, before its mechanism was understood. The importance of this for the maintenance and multiplication of the Desert Locust is obvious and appearances of large locust populations after an area has received a shower of rain loses its element of mystery.

The coveregence hypothesis accounts also for the regular seasonal movements of locust swarms between the areas receiving winter-spring rainfall and those subject to monsoon rains (Waloff, 1946; Donnelly, 1947; Davies, 1952; Fortescue-Foulkes, 1952). The value of such movements for the species is obvious.

If we remember the ability of the adult Desert Locust either to mature and lay eggs soon after becoming adult, or, in the absence of suitable conditions, to delay the maturation for several months, the risk of losses of its population through unfavourable climatic conditions appears less serious than one might conclude from its physiological requirements. There is no doubt that the instability of the environment and, in particular, the unreliability of rainfall in desert regions make the life of the Locust very precarious, but its mobility, linked up as it is with weather dynamics, helps it to overcome its physiological handicaps.

While these points are of general biological interest, they also have an important practical bearing. The Desert Locust is unquestionably one of the most important insect pests and its periodical swarming and invasions of fertile lands have always been associated with the neighbouring deserts, which were blamed as the source of swarms. Investigations of the last 20 years have not yet solved the problem of where and how exactly swarms arise from scattered locust populations, but there is enough evidence to state, in a general way, that swarm formation cannot occur in areas with persistent extreme desert conditions. The maintenance of locust populations in the desert depends on the existence of favourable ecological islands, be they permanent or seasonal, and such areas are dependent either on fairly regular seasonal rainfall or on run-off of rain water from highlands along seasonal river-beds, or, finally, on artificial irrigation. It is the latter which deserves our particular attention. There are already some observations suggesting the importance of irrigation and cultivation for creating or expanding habitats favourable for the Desert Locust. The land development scheme at Abyan, Aden Protectorate, has lately become an area with a fairly persistent population of Desert Locust and repeated efforts are required to keep it under control. Extensive cultivation areas in the Tokar delta on the Red Sea coast of the Sudan form a classical locality for the Desert Locust and it has to be kept under regular observation and control. In Tripolitania, the breeding by invading swarms in 1946 was mainly concentrated on reclaimed sand-dunes immediately adjoining cultivation (Brown, 1947). On the Red Sea coastal plains of Eritrea, Saudi Arabia and Yemen, locusts are normally found in the sandy deltas of seasonal rivers where native cultivation is extensive, if sporadic. Even in the heart of the desert, in the Fezzan, considerable breeding populations of locust, were found in spring 1952 in alfalfa cultivated on run-off water from the hills (K. Guichard, unpublished); and a similar observation was made in Mauretania (Bruneau de Miré, 1952).

These examples suggest that reclamation of desert areas, which is most likely to occur where the existing conditions already tend to create favourable locust habitats, may not be an unmixed blessing, by making such habitats more permanent and provided with a regular food supply for locusts. So far, this has happened only on a limited scale, e.g. in Abyan and in Tokar, but if desert reclamation is to bring substantial benefits, it has to extend to many more and to much wider areas, and the effects on Desert Locust populations may well assume very serious proportions. Somewhat parallel cases are not unknown. The Rocky Mountain grasshopper (*Melanoplus mexicanus* Sauss) can normally produce one annual generation in Arizona where it was not a serious pest until extensive irrigation and cultivation of alfalfa created a stable favourable habitat, making it possible for the grasshopper to produce several generations a year; regular chemical control keeps the pest within limits, but at a considerable annual cost (Uvarov, 1948).

It should not be concluded, of course, that desert reclamation is undesirable because it may encourage the locust, but this danger must be borne in mind when desert development schemes are considered. It should be possible to provide safeguards against undesirable consequences of irrigation and cultivation, but the need for such safeguards must be realised in time.

The above considerations refer to reclamation of the desert itself, but the effects of extension of cultivation in the marginal areas must also be mentioned with reference to locust danger. At present, the possibility of keeping the Desert Locust under permanent control still remains theoretical, and extensive anti-locust campaigns are necessary to prevent devastation of fertile regions by invading swarms. The strategy of these campaigns aims at achieving maximum destruction of locusts at a season when they are breeding in desert areas. To give a recent example, swarm breeding by the Desert Locust in spring 1952 occurred over some 10,000 sq. miles of Arabian deserts; large mechanised forces had to be used to control the infestation and some 9,000 hopper bands were exterminated. Swarms which would have arisen from these bands would have spread over the fertile cresent of Middle East countries north of Arabia, but not a single swarm was allowed to develop and crops were saved, although at the cost of great efforts and very high expenditure. If crops were closer to the breeding areas, it would have been extremely difficult to prevent their damage by hopper bands, and the deeper cultivation penetrates in the desert, the greater are the chances of serious losses during plague periods. Again, one should not argue against the extension of marginal agriculture, but it would be wise to realise the danger inevitably connected with it.

The main general conclusion which may be suggested by considering the Desert Locust in relation to desert reclamation, is that while the latter is certainly able to increase crop producing areas, it would also increase the risks of losing the crops, unless repercussions of reclamation on certain members of desert fauna, such as the Desert Locust, are realised clearly and before it is too late.

The Desert Locust was taken in this paper mainly as a better known example of desert fauna. There are many other members of that fauna which are also associated with favourable ecological islands in the desert. An artificial increase of the number

and extent of such islands through reclamation will inevitably create a number of new entomological problems, perhaps not as serious as that of the locust, but still deserving to be anticipated rather than merely overlooked or ignored.

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SUR L'ORIGINE ET LE DÉVELOPPEMENT DES INSECTES NUISIBLES AUX PLANTES CULTIVÉES DANS LES OASIS DU SAHARA FRANÇAIS

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Introduction

Au Sahara, l'agriculture se concentre autour des points d'eau, car aucune plante ne serait cultivable sans irrigation; ces points d'eau, lorsqu'ils sont suffisamment importants, constituent les *oasis.*

Sur l'ensemble du territoire saharien français, les oasis sont rares et clairsemées, on peut les comparer à des îles isolées dans un vaste océan (oasis d'El-Golea, d'In Salah, de Djanet, de Mauritanie, etc.) ou parfois à un 'archipel' comprenant des petits îlots rapprochés (oasis du Touat, du Gourara, de la Saoura-Zouzfana, Koufra, etc.) (Le terme d''archipel' a été utilisé par P. de Peyerimhoff pour désigner l'ensemble des oasis de Koufra isolés dans le désert libyque). Cet isolement n'exclut pas, comme nous le verrons plus loin, des rapports très étroits existant sur le plan faunistique, entre les oasis et le milieu désertique environnant.

Les oasis sont cultivées par des populations sédentaires qui sont pour la plupart d'anciens esclaves noirs ou 'harratines'* originaires du Soudan dont les conditions sociales et matérielles n'ont d'ailleurs guère changé depuis leur 'libération' mais, les populations nomades, presque toutes d'origine blanche (berbères, chleuhs, touaregs, maures, chambaas) sont le plus souvent propriétaires des terrains et des palmeraies. Le rôle des nomades est loin d'être négligeable dans la vie des oasis, car ce sont eux qui entretiennent les contacts entre les localités très éloignées les unes des autres, créent les échanges à travers le désert et transportent ainsi à des distances considérables des rejets de dattiers (*djébars*), des plantes nouvelles sous forme de grains, graines, boutures, etc. C'est de cette manière que le plus souvent les insectes nuisibles phytophages ont été véhiculés puis se sont acclimatés dans les différentes régions habitées par l'homme au Sahara. Ceci est particulièrement vrai pour les Cochenilles du palmier-dattier. (Cf. *infra*).

Les plantes cultivées en oasis sont toutes ou presque toutes introduites (y compris le palmier-dattier) et la plupart d'entre elles n'ont pas une origine africaine. Aucune plante cultivée ne possède une origine strictement saharienne, excepté quelques variétés de blé cultivées au Fezzan et à Koufra qui se sont différenciées *in situ* mais dont la souche initiale doit être recherchée ailleurs. Le palmier-dattier (*Phoenix dactylifera* L.) constitue la culture essentielle des oasis où il occupe actuellement près de 100,000 ha au Sahara français. L'importance des oasis s'établit suivant le nombre de dattiers en production qui s'y trouvent (ensemble des palmeraies européennes de l'oued Rhir: plus de 2,000,000; Ouargla: 1,000,000; Figuig: 350,0000; Colomb-Béchar: 100,000; Ihrir et Ahrar (Tassili): quelques centaines). Il est évident que le nombre des palmiers est en rapport étroit avec les

*Les 'rachetés'.

possibilités d'irrigation. Sous les palmiers pousse toute une strate de cultures fruitières et vivrières introduites des régions subtropicales et tempérées telles que le Grenadier, la Vigne, les arbres fruitiers, le Figuier, les *Citrus*, les Céréales (blé et orge principalement), le Maïs, le Sorgho, le Mil (Sud-Saharien), diverses légumineuses (Fève, Luzerne, Haricot, Pois chiche, Oignon) et des Légumes variés. On y trouve aussi le Tabac (variétés indigènes), le Cotonnier (vivace indigène), le Kif, le Piment, des plantes à condiment, etc. Auguste Chevalier considère le Sahara comme un centre d'Agriculture primitive. Il est bien difficile d'admettre cette théorie. Rien ne prouve en effet qu'il ait jamais existé au Sahara un centre d'Agriculture primitive (néolithique ou préhistorique) (archéologique de A. Chevalier) comparable à ceux de l'Égypte, de l'Abyssinie, de l'Afganistan, de la Mésopotanie, de l'Inde, de la Chine ou du Mexique. Tous les végétaux cultivés au Sahara y ont été importés à une époque relativement récente et il n'y existe aucune tradition paysanne. Les travailleurs de la terre sont presque tous des descendants d'anciens esclaves noirs venus du Soudan, soumis au travail forcé par des populations blanches conquérantes (arabes, berbères, maures, peulhs, etc.) essentiellement nomades qui ont conservé jusqu'à nos jours une véritable répulsion pour le travail du sol. Tous les vestiges humains du Sahara, notamment ceux si nombreux du néolithique récent, nous renseignent sur l'existence dans toute l'étendu désertique actuelle, de populations guerrières ou semi-guerrières qui vivaient de chasse, de peche ou de collecte de graines de végétaux spontanés. Aucune trace d'Agriculture n'y apparaît. Le Sahara ne figure pas non plus parmi les différents centres d'origine des plantes cultivées cités par Vavilow, 1949-50, *Chronica botanica*, **13**.

Il est évident que les conditions écoclimatiques qui règnent dans les oasis sont différentes de celles du désert environnant. L'humidité y est nettement plus élevée et plus constante (du fait de l'irrigation), la température plus égale, l'insolation moins grande, notamment pour la strate cultivée sous les dattiers, le sol plus meuble et plus riche en matières organiques du fait de la culture. Ces conditions permettent donc le maintien d'une flore et d'une faune différentes de celles existant dans le désert environnant; cependant, comme nous le verrons plus loin, à part quelques cas très particuliers, l'influence du climat désertique proprement dit élimine, même des oasis, un très grand nombre d'insectes nuisibles.

Les plantes cultivées dans les oasis hébergent toute une série d'insectes nuisibles phytophages, mais l'intérêt économique de ceux-ci est très inégal, il varie d'ailleurs d'une oasis à l'autre, et cette faune ne revêt nulle part un caractère de rigoureuse homogénéité.

I. *Les Differents Types D'Insectes Phytophages des Oasis.*

La faune des insectes nuisibles peuplant les oasis sahariennes est pauvre et dégradée si on la compare à celle existant ou nord et au sud du Sahara et vivant sur des plantes cultivées similaires. D'autre part l'inventaire des espèces nuisibles a été peu poussé et nous ne possédons encore que des renseignements fragmentaires sur l'ensemble de cette faune, établis le plus souvent par des rapports administratifs sans grande valeur scientifique, ou par des observations rapides effectuées par des voyageurs de passage. Les études détaillées et coordonnées

manquent, si bien qu'il est encore difficile d'avoir une idée précise sur la composition de la faune des espèces nuisibles qui peuplent les oasis. Ce travail préliminaire n'est qu'amorcé, un bon nombre de localités sahariennes n'ont encore jamais été visitées par les entomologistes.

Dans la mesure des connaissances actuellement acquises, on peut distinguer parmi les insectes phytophages nuisibles vivant dans les oasis deux types d'éléments d'origine nettement distincte comprenant, d'une part, les espèces *introduites* (la plupart cosmopolites) et, d'autre part, les espèces *adaptées* d'origine nettement saharienne.

(*a*) *Éléments introduits.*

Ces éléments sont constitués par une faune hétérogène d'espèces accidentallement introduites par l'homme à une époque plus ou moins récente. Ils comprennent principalement des insectes cosmopolites vivant dans les denrées alimentaires stockées (grains, graines, farines, dattes, fruits et légumes secs, etc.) et que l'on retrouve dans tous les pays; leur pullulation est généralement favorisée par de très mauvaises conditions de conservation existant dans les entrepôts sahariens (ce problème préoccupe le F.A.O. qui a délégué une mission en Libye pour étudier les moyens de protection des denrées alimentaires stockées contre les insectes).

Parmi les espèces les plus représentatives de ce groupement, il convient de citer *Oryzaephilus surinamensis* L. et O. *mercator* Fauv.* *Carpophilus hemipterus* L. qui vivent dans les dattes; *Tribolium confusum* Duv., *Sitophilus orizae* L. dans les farines et graines de céréales, pâtes alimentaires et diverses matières amylacées, les *Dermestes,* notamment *D. frischi* L., dans diverses matières organiques. Le Scolyte des noyaux de dattes *Coccotrypes dactyliperda* L. n'est pas saharien, il vit dans les dattes immatures du Tell algérien et dans les graines d'autres palmiers, notamment de *Phoenix canariensis.* Il est très commun dans les jardins de la région méditerranéenne (Nord et Sud). Parmi les Lépidoptères, les *Ephesthia* (farine) et les *Myelois* (dattes) sont les plus fréquents. *M. decolor* Z. serait plus spécifiquement saharien et contaminerait les dattes mûres sur les arbres pour se développer ensuite dans les entrepôts alors que *M. ceratoniae* Z. (= *phoenicis* Dun.) est une espèce cosmopolite vivant sur tous les fruits desséchés (dattes, caroubes, figues, abricots, etc.) (Real, 1948).

On pourrait ajouter à cette liste beaucoup d'autres espèces d'intérêt secondaire.

En réalité il existe relativement peu de vrais phytophages nuisibles d'origine extra-saharienne introduits dans les oasis, et ceci est dû en grande partie au climat saharien caractérisé par une sécheresse atmosphérique et des maxima de température très élevés en été, de grandes fluctuations journalières et saisonnières empêchant le maintien de nombreux phytophages originaires des régions non désertiques du globe. D'autre part, les introductions par caravane nécessitent des transports de longue durée et le maintien d'une nourriture vivante fraîche pour les

* Ce dernier apparaît comme une simple forme du précédente (P. de Peyerimhoff).

insectes transportés; or ces conditions ne peuvent guère se trouver réalisées que pour les espèces vivant sur des rejets de dattiers, des graines, des grains, des bois vivants, des fruits desséchés et autres denrées alimentaires stockées. Tous les phyllophages, radicicoles floricoles, cécidogènes, mineurs de feuilles ou de tiges, suceurs de sève, ne peuvent supporter les voyages de longue durée et se trouvent éliminés au cours des longs transports par caravane. Il va de soi que les oasis ayant un contact plus étroit et plus constant avec la civilisation, notamment celles situées le long des lignes de chemin de fer (oasis du Nord) ou les grandes pistes sahariennes automobiles, sont plus soumises aux introductions nouvelles que les oasis éloignées, situées en dehors de toute voie de communication fréquentée. De même, aujourd'hui, l'avion favorise les nouvelles introductions d'insectes. Aussi le nombre des espèces extra-sahariennes introduites est proportionnellement plus élevé dans les oasis de la bordure nord du Sahara en particulier les oasis de la rive Sud du Sahara en contact avec les zones de cultures permanentes soudanaises où l'on trouve déjà bien fixés divers éléments cosmopolites n'existant pas encore ailleurs dans le désert: présence de la Mouche des fruits (*Ceratitis capitata* Wied.) à Biskra, d'*Icerya Purchasi* Mask. à Biskra et Laghouat, de la Teigne du poireau (*Acrolepia assectella* Z.), du Puceron noir des fèves (*Aphis fabae* Scop.), de divers *Pseudococcus* dans presque toutes les oasis Nord sahariennes et présahariennes du Sud de l'Atlas. Il existe des *Pseudococcus* indigènes au Sahara, notamment *Planococcus tuaregensis* Balachw. que j'ai décrit du Tassili (Amaïs) vivant sur *Ficus salicifolius* var. *teloukat* Batt. et Trab.

Les Cochenilles du palmier-dattier. L'origine exacte du palmier-dattier (*Phoenix dactylifera* L.) reste encore imprécise mais la majorité des botanistes (dont René Maire) sont d'accord pour considérer la zone désertique orientale (Iraq, Mésopotamie) comme sa patrie originelle. Sa culture au Sahara remonte à une époque fort ancienne et pour certaines oasis du moins, bien antérieure à l'invasion arabe.

Le dattier est parasité au Sahara par trois Cochenilles dont deux (*Parlatoria Blanchardi* Targ. et *Phoenicococcus Marlatti* Ckll.) lui sont spécifiques. *P. Blanchardi* est seul réellement nuisible; c'est une espèce strictement désertique qui ne peut se maintenir en dehors du climat saharien ou subsaharien. Son aire de répartition coïncide étroitement avec la zone de maturation naturelle des dattes. Sur le littoral méditerranéen, où le dattier est fréquemment cultivé comme arbre d'ornement, on ne trouve la Cochenille nulle part; il en est de même pour le Tell et les Hauts-Plateaux. A l'exception d'Inkermann et d'Orléansville dans la vallée du Chéliff (Algérie) où des dattiers contaminés originaires de Biskra ont été introduits en 1928 et plantés le long de la gare (A. Perrin). Le climat de la vallée du Chéliff est un des plus chauds du Tell algérien et caractérisé par des maxima très élevés en été (+ 40°C); ces conditions exceptionelles pour le Tell ont permis vraisemblablement le maintien permanent ou subpermanent de *P. Blanchardi*. La même remarque s'applique pour la rive Sud du Sahara où, hors de la zone saharienne, le dattier est indemne de Cochenilles (région de Garoua-Maroua, Nord-Cameroun et dépression du Tchad). *P. Blanchardi* existe dans l'Aïr, l'Adrar des Iforas et dans cer-

taines oasis du Tibesti (Gourmeur). Nous ne l'avons pas trouvée sur les dattiers de la région du Tchad où elle a été signalée dans le Borkou (mission antiacridienne de 1934.

Au Sahara proprement dit, la Cochenille existe partout excepté dans les oasis occidentales. Elle fait défaut encore dans la plupart des oasis marocaines (Bani – Draa – Tafilalet), dans celle de la Saoura-Zouzfana, du Gourara (y compris celles du Tinerkouk), du Taouat à l'exception de quelques localités où son introduction est récente (Colomb-Béchar: 1920; certaines oasis du Touat:. 1912; Tata-Maroc: 1945). Cette aire de répartition confirme la théorie de l'origine orientale du dattier; sa progression de l'Est vers l'Ouest au Sahara ayant été plus rapide que celle de la Cochenille qui a suivi son hôte avec plusieurs siècles ou plusieurs dizaines de siècles de retard. Mais, même dans la zone d'invasion ancienne, certaines oasis particulièrement isolées et sans contacts avec la civilisation, restent encore indemnes de Cochenilles, comme c'est le cas pour la vallée d'Ahrar dans le Tassili N'Ajjer. Il est hors de doute que le rôle de l'homme fut prépondérant dans ces introductions et toute idée 'd'invasion naturelle progressive' de proche en proche doit être exclue étant donné la discontinuité de la répartition géographique du dattier dans le Sahara et la spécificité rigoureuse de *P. Blanchardi.*

En ce qui concerne *Phoenicococcus Marlatti* Ckll., bien que son origine désertique ne puisse être mise en doute, son aire de répartition est beaucoup plus vaste, car cette Cochenille a suivi le dattier un peu partout où il a été introduit, y compris dans les nombreux parcs, jardins, avenues, de la région méditeranéenne (Alger, Tunis, Antibes, Elche, Palerme, etc.). *P. Blanchardi* et *Ph. Marlatti* ont été introduits aux États-Unis (Arizona, Californie du Sud) avec des djebars de 'deglet nour' originaires du Sahara algérien et tunisien. Après 30 années d'efforts, les américains ont éliminé *P. Blanchardi* de leur territoire: Boyden, B.L. Eradication of *Parlatoria* date scale in the United States (*U.S. Dept. Agric. Mix. publ. No. 433 Wash,* D.C. 1941). Enfoncée dans les gaines foliaires, à l'abri de la lumière et de l'insolation, cette espèce se trouve dans des conditions microclimatiques totalement différentes de celles de *P. Blanchardi*, localisé sur le feuillage et soumis directement à une intense insolation. On est encore mal renseigné sur la 'qualité' de la lumière du désert, la même remarque s'applique pour les autres régions de l'Afrique. Il s'agit cependant là d'un facteur écobiologique d'une importance considérable. Nous savons seulement que la lumière du désert est riche en radiations appartenant à la zone droite du spectre (bleu à ultra-violet). Cet habitat suffit à démontrer les possibilités d'adaptation de *P. Marlatti* à des climats non désertiques.

Enfin une troisième espèce a été signalée sur le dattier bien que sa présence y paraisse accidentelle, c'est *Pseudaspidoproctus hyphaenicus* Hall, *Margarodidae* décrit d'Égypte sur le palmier-doum (*Hyphaene thebaica*) (Hall, W.J., 1926). Cette Cochenille est répandue dans diverses oasis d'Egypte et elle a été trouvée dans celle de Bendleia dans le Fezzan sur palmier-dattier, par F. Bernard (Rungs C., 1944).

Le palmier-doum est d'origine tropicale, il fait partie de la flore sahélienne mais il a été cultivé autrefois au Sahara pour ses fruits et se retrouve à l'état de

pieds isolés dans quelques oasis du Fezzan et du désert égyptien. Chevalier le considère comme une relique de l'agriculture au Sahara où sa présence doit être considérée comme très ancienne et a sans doute précédé celle du dattier. A notre avis, la présence du Doum au Sahara constitue une relique d'un passé plus humide, de l'époque où la flore sahélienne actuelle avait une extension continue et homogène presque jusqu'en Afrique du Nord, à travers le Sahara actuel (quaternaire récent). Le passage de la Cochenille du Doum au Datteir s'est fait certainement *in situ*, lorsque ces deux plantes ont été en contact dans les oasis. Il existe une 4[e] espèce spécifique du palmier-dattier décrits de Mésopotamie, *Asterolecanium phoenicus* Ram. Rao. Elle n'a pas pénétré jusqu'ici en Afrique et son rôle économique paraît négligeable.

(*b*) *Éléments adaptés.*

Ils sont constitués par des espèces phytophages saharienne vivant normalement aux dépens de la flore spontanée du désert. Ils préexistaient donc à la création des oasis même, mais celles-ci leur ayant apporté des conditions de vie plus favorables (végétation plus abondante, humidité plus régulière, sol plus meuble), leur pullulation a été favorisée dans ces stations par la culture et il y a eu un phénomène d'attraction. Cependant tous ces éléments se retrouvent dans le désert proprement dit en dehors des oasis, principalement dans les lits d'oued, autour des gueltas, dans les cañons où une humidité plus élevée se maintient en permanence. Parmi ces collections d'insectes, il y a lieu de distinguer d'abord les *Phytophages polyphages à régime varié* représentés principalement par des espèces aux moeurs radicicoles ou subradicicoles appartenant à différents ordres ou familles d'insectes: *Orthoptera, Scarabaeidae, Noctuidae,* etc. En dehors de ces types on en trouve d'autres à régime plus strict, *spécifique* ou *subspécifique*, qui vivent dans le désert aux dépens de plantes de la même famille botanique que celles cultivées en oasis. Enfin, il existe une troisième catégorie d'éléments particulièrement intéressants vivant normalement sur la flore spontanée et qui se sont *adaptés* à la flore cultivée lorsque celle-ci est apparue dans les oasis. Ces passages constituent de véritables exemples d'allotrophie et démontrent d'une manière suggestive le processus de formation d'espèces nuisibles aux dépens de types sauvages considérés jusqu'ici comme économiquement indifférents.

(i) *Phytophages polyphages des oasis.* — Nous passerons ici volontairement sous silence tout ce qui se rapporte aux Acridiens migrateurs, le problème acridien n'étant pas strictement saharien. On trouve par contre dans les oasis de nombreux Orthoptères polyphages et parmi ceux-ci, il convient de citer divers Gryllides et Gryllotalpides, notamment les Courtillères (*Gryllotalpa gryllotalpa* L. et *Grylotalpa africana* Beauv.) et un gros grillon principalement répandu dans les oasis du Sahara central et oriental, *Brachytrypes megacephalus* Lef.

Les Courtillières dévastent les jardins irrigués dans les oasis; on trouve dans le Nord principalement *G. gryllotalpa* L. (grosse Courtillière) alors que dans le Nord comme dans tout le reste du Sahara ainsi que sur l'ensemble du continent africain on trouve *G. africana* Beauv. (*petite Courtillière* qui a des moeurs presque identiques(*G. gryllotalpa,* bien que d'origine paléarctique, pénètre profon-

dément dans le Sahara, Pasquier signale sa présence au Fezzan.). Ces espèces se retrouvent dans les lits d'oueds sablonneux non cultivés, autour des gueltas dans les terrains humides et les sols légers, opérant de la même manière que dans les oasis. Quant au *Brachytrypes*, très répandu dans les oasis du Fezzan, c'est un très gros grillon qui creuse de profondes galeries et dévore les plantes durant la nuit. (Pasquier 1951). Cet insecte est également répandu dans le Sahara soudanais. Il existe en Tunisie, en Algérie (Bône) et en Sicile où il constitue une 'relique' tropicale; signalé des oasis de Touggourt et Ouargla (Dr Jacquemin). On trouve également dans les oasis quelques Orthoptères se rencontrant normalement dans les lits d'oueds desséchés sur des plantes sauvages, principalement les Graminées, et qui, dans les lieux cultivés, dévastent le feuillage du Mil et du Maïs, comme c'est le cas pour *Euprepocnemis plorans* Charp., acridien largement répandu sur le territoire africain, y compris le Sahara et pour *Poekilocerus hieroglyphicus* Klug. Ce 'catoué' saharien et soudanais de couleur jaune, aux ailes orange vif, est considéré par divers auteurs comme spécifique du *Calotropis procera*. Au Tassili n'Ajjers nous l'avons observé dans les lits d'oued, dévorant des touffes de graminées alors que les *Calotropis* faisaient complètement défaut. *Zonocerus variegatus* L. le 'Catoué' d'Afrique tropicale ne dépasse pas au Nord de la zone sahélienne. Les larves de *Scarabaeidae*, notamment des *Melolonthinae*, *Cetoniinae* et *Dynastinae*, se rencontrent fréquemment dans les cultures sahariennes. Parmi les premiers qui seuls sont véritablement phytophages et radicicoles, il y a lieu de citer les *Rhizotrogus* (s.l.), mais ce genre si richement représenté en Berbérie (64 espèces) ne pénètre guère dans le désert; il se rencontre seulement dans les oasis septentrionales en bordure de la steppe. Comme l'a fait si bien ressortir P. de Peyerimhoff (1945), les *Rhizotrogus* nord-africains, presque tous endémiques, sont en réalité des espèces des hauts plateaux algéro-tunisiens où les ravages de leur larves s'exercent intensément parmi les cultures de Céréales. Peu d'espèces pénètrent dans le désert proprement dit et le groupe se raréfie aussi à l'Est où il ne dépasse par la Cyrénaïque; aucune espèce n'est connue d'Égypt. Le genre est également assez pauvrement représenté à l'Ouest (Maroc).

Les *Dynastinae* sont surtout représentés par des espèces rudérales vivant dans le terreau et principalement dans celui qui s'accumule à la cime des palmiers à la base des gaines foliaires. On trouve ainsi dans toutes les oasis *Phyllognatus excavatus* Forst. ('doudd' ou 'doudda' des Arabes) signalé bien souvent à tort comme nuisible; c'est beaucoup plus (dans les oasis) une espèce détriticole que réellement phytophage. Dans d'autres régions, les larves de *Phyllognatus* sont nettement phytophages radicoles. Cf. Balachowsky, A. et Mesnil, L. 1936. Les insectes nuisibles aux plantes cultivées, t. II, p. 659, Paris. De même, les *Pentodon* (*P. deserti* Heyden et *P. bispinosus* Kunt.) existent dans tout le Sahara; leurs larves sont communes parmi les cultures des oasis (Hoggar, Fezzan, Koufra, Oued Rhir, Djerid, etc.). Elles fréquentent surtout les terres riches en matière organique et détruisent les plantes en les coupant au-dessus du collet. Leurs dégâts sont toujours sporadiques et isolés.

Parmi les *Cetoniinae* il convient de citer les larves de *Pachnoda Savignyi* G. et P. qui existent dans le Sahara central et soudanais (Tassili, Fezzan, Koufra) vivant comme *Phyllognatus excavatus* dans le terreau de la cime des Dattiers: cet habitat n'est certainement pas exclusif. Les adultes butinent les fleurs en compagnie d'autres Cétoines, notamment d'*Oxythyrea pantherina* Gory et *Tropinota squalida* L.; elles sont fréquentes sur les fleurs épanouies d'*Acacia seyal* et d'*Acacia raddiana*.

Les Nocteules sont fréquentes dans les oasis et leurs larves s'attaquent à toute espèce de plante cultivée, principalement aux légumes, sans avoir un régime spécialisé. On trouve au Sahara des espèces du g. *Plusia, Prodenia, Laphygma, Chloridea,* etc., qui ont une aire de répartition très vaste à travers le continent africain. Elles se rencontrent non seulement dans les oasis, mais aussi en dehors de celles-ci, en plein désert sur des plantes spontanées (*Plusia gamma* L.; *Laphygma exigua* Hb.). *Rhycia protophila* Guen. est une espèce plus strictement nord-saharienne, nuisible dans les oasis du Sahara marocain (Rungs). Il y a lieu également de signaler des dégâts de *Arenipses sabella* Hmps. (*Gelechiidae*) dont la chenille de 4 cm de long, brunâtre, s'attaque au jeune régime de dattier avant sa sortie du spathe. Il se produit une nécrose caractéristique pourrissant la fleur. J'ai observé cette espèce à El-Golea en avril-mai 1926 et elle est également commune à Timimoun et Adrar (Gourara-Touat).

(ii) *Éléments spécifiques ou subspécifiques.* — Ce sont des phytophages à régime plus strict, vivant au Sahara sur des plantes spontanées bien déterminées ou liées à une famille botanique; ils se sont adaptés en oasis à des plantes botaniquement voisines ou de la même famille. L'on a affaire ici à de véritables collections de phytophages passant sur la végétation cultivée avec toutes leurs cohortes de commensauz, parasites et satellites.

Les Piérides (*P. rapae* L. et *P. napi* L. en particulier) dévastent fréquemment les cultures de Crucifères en oasis (navets, raves, choux, etc.) et elles vivent dans le désert aux dépens de divers Crucifères sauvages. Les Punaises des Crucifères, notamment les *Eurydemna,* obéissent aux mêmes règles.

Sur les Contonniers vivaces cultivés en oasis on trouve toute la faune émigrée des Malvacées sauvages du désert, notamment des *Malva* et des *Althea,* particulièrement les Punaises *Oxycarenus* auxquelles viennent s'ajouter dans la zone Sud-Saharienne des *Dysdercus.*

L'étude des Aphides vivant au Sahara pose un problème plus complexe depuis que des travaux récents ont dissocié des espèces telles que *Aphis craccivora* Koch (= *A. laburni* des auteurs, non Kalt) considérées autrefois comme polyphages sur les Légumineuses et même sur les plantes d'autres familles.

Les plantes désertiques spontanées, constituant l'habitat des Aphides, forment souvent des 'relais' permettant à l'espèce non seulement de se maintenir, mais encore de traverser le désert et d'occuper ainsi une aire de répartition continue extrêmement vaste à travers le continent africain. C'est ainsi que *Rhopalosiphum nymphaeae* L., si commun en Europe et dans la région méditerranéenne

sur les plantes aquatiques les plus variées, se maintient au Sahara central sur les *Potamogeton* où nous l'avons trouvé dans les gueltas du Tassili N'Ajjer (Dider), loin de toute culture. Il est probable que cette espèce se maintient au désert uniquement par la forme émigrante, car l'œuf d'hiver est pondu sur des *Prunus* dont il n'existe aucun représentant parmi la flore désertique spontanée. Le *Potamogeton* constitue donc un véritable 'relais' permettant à *Rhopalosiphum nymphaeae* d'avoir une aire de répartition continue depuis l'Afrique du Nord jusqu'au Soudan. *Aphis nerii* F. vit sur *Nerium oleander* dans le Sud de l'Europe et le Nord de l'Afrique; on le retrouve sur cette plante au Sahara le long des oueds, mais le Laurier rose n'existe pas partout dans le désert et se raréfie au fur et à mesure que l'on approche du Sahara central; l'espèce passe alors sur *Calotropis procera* qu'elle suit dans son aire de répartition vers le Sud jusque dans la zone des savanes tropicales (région du Tchad). Les deux espèces que nous venons de citer ne sont pas réellement nuisibles, mais elles constituent des exemples typiques valables pour d'autres espèces qui peuvent trouver des *relais* constitués par des plantes sauvages sahariennes, sur lesquelles leur développement est parfaitement possible. Un exemple analogue nous est fourni par la Coccinelle du Melon (*Epilachna chrysomelina* F.) qui vit dans la zone méditerranéenne sur diverses Cucurbitacées sauvages et cultivées, occasionnant de sérieux dégâts aux cultures de Melons et Pastèques dans le Tell algérien. Cette espèce a une aire de répartition très vaste, jusqu'au Soudan, et traverse le Sahara sur sa 'plante relais', la Coloquinte (*Colocynthis vulgaris* Schred.) sur laquelle nous l'avons trouvée au Tassili, loin de toute culture. Chopard signale également sa présence dans l'Aïr sans préciser son habitat dans cette région et P. de Peyerimhoff au Hoggar et dans le Fezzan sur la Coloquinte.

Lorsque ces 'relais' botaniques n'existent pas, l'expansion des phytophages nuisibles dans le désert est soumise à des facteurs artificiels, dont le principal est le transport accidentel par l'homme.

L'absence de 'plantes relais' pour certaines espèces suffit à expliquer les lacunes considérables existant parmi la faune des Pucerons nuisibles dans les oasis. C'est ainsi que le Puceron noir des Fèves, *Aphis fabae* Scop., les Pucerons des arbres fruitiers (Abricotier, Prunier), les Pucerons vivant sur la Tomate, sur le Tabac, n'existent pas dans l'oasis de Djanet ni dans les autres oasis du Sahara central que nous avons visitées à une saison favorable, alors que ces insectes pullulent dans les oasis nord-sahariennes. Cette absence fait ressortir non seulement l'importance du rôle joué par les 'plantes relais', mais aussi que des facteurs atmosphériques tels que les vents violents qui soufflent au Sahara ne suffisent pas à véhiculer les Pucerons à travers le désert. Bien que des Aphides aient été trouvés jusqu'à 3,000 m d'altitude dans les recherches effectuées sur la 'faune atmosphérique' dans d'autres régions du globe, le vent ne paraît pas pouvoir les véhiculer du Tell aux oasis du Sahara central. Quant aux posibilités du maintien des Pucerons d'origine non saharienne dans les oasis, elle est certainement possible, car bien des espèces sont susceptibles de vivre et d'évoluer sous les climats les plus variés. Un

grand nombre d'Aphides nuisibles pullulent dans les cultures de moyenne et de haute Égypte dont les conditions écobiologiques sont à peu près identiques à celles des oasis sahariennes.

(iii) *Éléments récemment adaptes.* — Dans cette dernière catégorie, la plus intéressante à notre avis, se groupent quelques espèces vivant normalement au Sahara sur des plantes sauvages spontanées et qui se sont adaptées brusquement à des plantes cultivées en oasis lorsque celles-ci se sont trouvées à leur contact. Les éléments 'récemment adaptés' constituent le fond de la faune des insectes phytophages nuisibles de l'Afrique tropicale et équatoriale. Les ¾ des espèces vivant actuellement en Afrique noire sur les plantes cultivées (elles-même presque toutes introduites) proviennent d'adaptations récentes ou toutes récentes (certaines d'entre elles continuent à se produire à l'heure actuelle) d'espèces vivant primitivement sur des plantes sauvages de la savane ou de la forêt. Certaines de ces adaptations constituent de véritables exemples d'allotrophie et une démonstration suggestive de la formation sous nos yeux d'espèces nuisibles aux dépens de types n'ayant pas d'intérêt agricole. Les exemples les plus typiques nous sont fournis par diverses Cochenilles *Diaspidinae.*

Saharaspis Ceardi Balachw. vit normalement sur les *Ziziphus* sauvages au Sud de l'Atlas, mais il s'est adapté dans toute la zone Nord du Sahara aux arbres fruitiers cultivés en oasis, notamment à la Vigne, à l'Olivier, au Figuier, au Murier, au Caroubier, etc. On le trouve depuis le Sahara marocain océanique jusqu'en Tunisie. Dans certaines oasis notamment dans cette de Tarjicht (oasis présaharienne de l'Anti-Atlas marocain), nous avons trouvé cette espèce attaquant avec vigueur des cépages de Vigne indigène cultivée, déterminant le desséchement des sarments. *S. Ceardi* a été trouvé par les entomologistes marocains en dehors de la zone saharienne, notamment à Salé (env. Rabat) sur Mûrier, ce qui prouve qu'il est susceptible, maintenant qu'il est adapté aux végétaux cultivés, d'étendre considérablement son aire de répartition vers le Nord.

Une autre espèce que nous avons décrite du Hoggar, *Aspidaspis Laperrinei* Balachw., vivant sur *Olea-Laperrinei* à 2,400 m d'altitude se retrouve sur ce même Olivier et d'autres plantes dans l'étage méditerranéen du Tassili N'Ajjer, notamment sur *Myrtus nivellei* et *Nerium oleander* (1,400-1,700 m d'altitude). Il s'agit donc d'une espèce polyphage indigène inféodée aux massifs du Sahara central. (Cette espèce a été retrouvée récemment par Kaussari dans le Sud de l'Iran (Béloutchistan iranien) sur *Calligonum* sp.). Dans l'oasis d'Ihrir et dans celle de Djanet, nous avons trouvé *A. Laperrinei* adapté sur des plantes cultivées, notamment à la Vigne, l'Abricotier, le Rosier et le Grenadier, dans le jardin de la Direction des Affaires indigènes. Il s'agit là d'une adaptation toute récente, ces plantes ayant été introduites dans cette oasis il y a une dizaine d'années.

Sur la rive Sud du Sahara nous avons des exemples analogues avec *Octaspidiotus Dallonii* Balachw., *Aspidiotini* décrit de l'oasis de Gourmeur (Tibesti) vivant sur *Ficus salicifolius;* cette espèce a été trouvée dans l'oasis de Myrriah

(environs de Zinder) par Remaudière, sur des Goyaviers cultivés (adaptation récente).

Les trois exemples que nous venons de citer démontrent que des espèces considérées jusqu'ici comme n'ayant aucun intérêt agricole sont en voie de devenir nuisibles. Il est probable que si ces insectes, qui sont intensément parasités au Sahara par leurs ennemis naturels, étaient introduits dans d'autres régions du globe, leur nocivité se trouverait considérablement accrue. Ils possèdent en eux-même un potentiel de nocivité permanent démontrant la nécessité d'étudier bien davantage la biologie des phytophages vivant sur les plantes spontanées en vue de leurs possibilités de passage sur les végétaux cultivés. Une fois de plus ces problèmes apparaissent comme intimement liés.

II *État Phytosanitaire Des Oasis Sahariennes.*

Dans la limite où l'inventaire des insectes nuisibles a été fait dans les différentes oasis du Sahara français, l'état phytosanitaire de celles-ci n'apparaît nulle part comme revêtant un caractère réel de gravité, tout au moins en ce qui concerne les insectes nuisibles. Exception fait pour les espèces vivant aux dépens des denrées alimentaires stockées dont les ravages posent des problèmes particuliers; la nocivité des vrais phytophages est réduite, elle ne s'exerce jamais d'une manière généralisée à caractère épidémique entraînant des catastrophes économiques ou sociales pour ces régions, déjà très déshéritées en elles mêmes. En ce qui concerne les Acridiens migrateurs, la seule espèce qui vit réellement au Sahara est le Criquet pèlerin (*Schistocerca gregaria* Forsk.) qui traverse entièrement le désert, soit dans la direction Sud-Nord ou Sud-Est-Nord-Ouest, suivant que les essaims partent de l'Atlantique ou de la mer Rouge. Ce sont les formes adultes qui, s'abattant dans les oasis, provoquent par les années d'invasion des dégâts considérables en dévorant toutes les cultures.

Les oasis présahariennes et celles situées en bordure de l'Atlas saharien sont généralement beaucoup plus dévastées que les autres du fait que les Criquets arrivent dans ces régions alors qu'ils sont déjà à un âge avancé (Sauterelles jaunes) et dans une phase d'alimentation intense. Les essaims venant directement du Rio del Oro apparaissent au Sahara sous la forme jeune (Sauterelles roses) et ne s'alimentent pas. Ces vols traversent en général l'Atlas pour effectuer leurs pontes, et c'est à ce moment-là que l'espèce se montre nuisible, tant à l'état adulte qu'à l'état larvaire.

Quant au Criquet migrateur, *Locusta migratoria* L., ph. *migratorioides,* il ne dépasse pas au nord la zone sahélienne soudanaise; c'est une espèce presque exclusivement graminicole. L'ensemble de cette faune est faiblement agressive du fait qu'elle est tenue en échec par de dures conditions écologiques et aussi par un parasitisme intense qui s'exerce partout au Sahara, aussi bien dans les oasis que dans le milieu désertique proprement dit. Au Sahara, la vie a atteint presque partout un équilibre stable et statique.

Il est également peu probable que des introductions nouvelles se produisent, excepté peut-être pour quelques Aphides ou Coccides (cf. *supra*) en raison des

conditions écobiologiques très particulières qui régnent au Sahara, rendant la vie des phytophages non sahariens et leur adaptation, précaire ou impossible.

Un autre facteur favorable est constitué par l'isolement des oasis les unes par rapport aux autres, il serait toujours possible de détruire ou de réduire les dégâts d'une espèce dangereuse au cas où elle apparaîtrait dans l'une d'elles; il serait également facile d'empêcher sa propagation par l'application de mesures phytosanitaires élémentaires. L'exemple de la progression très lente de *P. Blanchardi* dans le Sahara occidental est démonstratif à ce point de vue.

Telle qu'elle apparaît dans la limite des connaissances actuellement acquises, cette faune présente des lacunes considérables, si on la compare à celle qui vit sur les mêmes végétaux cultivés, hors de la zone saharienne. Un nombre considérable d'éléments manquent, notamment de très nombreux Pucerons nuisibles (cf. *supra*), la plupart des Cochenilles nuisibles (toutes les Cochenilles des Agrumes disparaissent au Sahara (El Golea, Mzab, oued Rhir)), des Thysanopteres, des Coléoptères phytophages (*Curculionidae, Chrysomelidae*), dont certaines familles (*Scolytidae*) font même totalement défaut, la plupart des Lépidoptères nuisibles non polyphages, etc. Cet état de choses fait ressortir à quel point cette faune est restée à l'abri des introductions et des acclimatations. Certaines cultures, telles que les Céréales (sur pied), ne possèdent au Sahara pour ainsi dire aucun insecte parasite important (en dehors des polyphages). Quant au nombre des endémiques sahariens nuisibles, il est également très faible, les éléments adaptés sont récents et leur nocivité apparaît encore comme peu accusée.

En dehors du climat saharien proprement dit, il existe certainement d'autres facteurs qui contribuent à l'élimination ou la limitation numérique des espèces nuisible dans leur oasis.

Le 'rythme vital' presque exclusivement nocturne pour les espèces sahariennes, est défavorable aux espèces à 'rythme diurne', c'est-à-dire à la grande majorité des espèces nuisibles phytophages. L'insolation proprement dite avec sa lumière riche en radiations violettes et ultra-violettes influence certainement défavorablement le développement des œufs ou des jeunes larves de nombreux phytophages. De même l'échauffement du sol en surface, surtout lorsqu'il est sablonneux et léger, où il peut atteindre des températures critiques de mort des insectes (+ 60 à 70°C) constitue en facteur éminemment préjudiciable à la nymphose de nombreuses larves de phytophages qui s'opère à une très faible profondeur dans le sol.

Enfin, la grande majorité des insectes sahariens possède de longues diapauses qui leur permettent de passer les périodes critiques ou défavorables même si elles se prolongent pendant plusieurs années consécutives (Cochenilles-*Margarodes*). Il n'en est pas de même pour la plupart des insectes phytophages introduits dont l'éthologie n'accuse pas d'arrêts de développement. Ces espèces se trouvent donc obligées d'évoluer dans des conditions très défavorables, notamment pendant la période estivale chaude où la vie est normalement très ralentie au Sahara, surtout pendant la phase diurne.

La pauvreté des phytophages sahariens apparaît également pour les insectes vivant aux dépens des végétaux spontanés. Ce phénomène est particulièrement

accusé pour la faune des espèces végétales 'reliques' qui subsistent dans certaines stations limitées ou très limitées du Sahara, comme les témoins précaires d'un passé plus humide ou plus frais. *Olea Laperrinei* Batt. et Trab., olivier sauvage de l''étage méditerranéen' du Hoggar et du Tassili, n'héberge pour ainsi dire aucun phytophage en dehors d'une cochenille – *Diaspidinae* (*Aspidaspis Laperrinei* Balachw.) rare et clairsemée dans les peuplements spontanés. Son 'correspondant' méditerranéen, l'Oléastre (*Olea europea* L.) est habité par contre par près d'une centaine d'espèces de phytophages spécifiques ou subspécifiques de tous ordres. Il en est de même pour *Myrtus Nivellei* du Tassili et du Hoggar qui n'est attaqué par aucun insecte, alors que son 'correspondant' méditerranéen, *Myrtus communis* L. est très parasité,

Cupressus Dupreziana Camus, le magnifique cyprès du plateau de Tamrit (1,750 m) dans le Tassili (Sahara central), représenté aujourd'hui par une centaine d'individus presque tous millénaires ou plusieurs fois millénaires, n'est attaqué par aucun insecte xylophage ni phytophage comme nous avons pu le constater en étudiant cette 'station relique' en mai 1949. Son 'correspondant' du Haut-Atlas marocain, *Cupressus sempervirens* L. (= *atlantica* Gaussen) possède par contre toute une faune de phytophages spécifiques ou subspécifiques.

Si l'on étudie la biocoenose des 'émigrés tropicaux' sahariens venus du sud, on arrive à des conclusions identiques. *Ficus salicifolius* Vahl. ssp. *Teloukat* Batt. et Trab. est un *Ficus* tropical qui remonte jusqu'au Sahara central (Tassili); il est loin de renfermer la riche faune des *Ficus* tropicaux, c'est à peine s'il héberge trois ou quatre espèces d'insectes dont un Lépidoptère mineur de tige, un *Aleyrodidae* et une cochenille, *Pseudococcini*. Sur *Balanites aegyptica* Delile du Sahara central nous n'avons rien trouvé alors que cette plante héberge toute une faune particulière dans la zone sahélienne du Tchad et de l'A.O.F. Rien non plus sur *Salvadora persica* L. en dehors d'un *Aleyrodidae*.

Les Acacias épineux du Sahara (*Acacia raddiana* Savi, *Acacia seyal* Delile) forment aujourd'hui un reliquat dégradé de la brousse sahélienne qui s'est étendue autrefois beaucoup plus vers le nord. L'étude de leur biocoenose fait apparaître une faune considérablement appauvrie par rapport à celle du Soudan, du Niger ou du Tchad. Cet appauvrissement s'accuse au Sahara même, du sud vers le nord; dans la Soura, le Djebel Bechar ou l'Anti-Atlas marocain, les *Acacias* ont perdu presque toute leur riche faune originelle tropicale.

Tous ces végétaux qui subsistent aujourd'hui dans des conditions différentes de celles de leur milieu naturel ont rapidement perdu leurs insectes phytophages spécifiques ou subspécifiques qui n'ont pu résister au changement de climat ni s'adapter aux dures conditions sahariennes. Dans certains cas, cette élimination a été totale, comme pour *Cupressus Dupreziana* Camus, qui est devenu une espèce végétale 'azoïque'.

Il est probable que lorsque l'écologie saharienne sera mieux connue, les facteurs limitatifs jouant en défaveur des insectes phytophages nous apparaîtront avec beaucoup plus de clarté.

Quoi qu'il en soit, si les rendements sont faibles au Sahara et certaines cultures très déficitaires, cela ne tient pas spécifiquement aux attaques des insectes nuisibles, mais à d'autres causes beaucoup plus importantes. La pauvreté organique du sol, la très mauvaise qualité des graines de semence ne subissant non seulement aucune sélection par rapport au milieu, mais souvent même aucun renouvellement, leurs très mauvaises conditions de conservation, et enfin leur plantation dans un sol constamment épuisé, sont autant de facteurs qui contribuent à la pauvreté des rendements sahariens, Certaines maladies cryptogamiques sévissent également avec intensité, notamment les Charbons des Céréales. Dans certaines localités (vallée d'Ahrar), plus de 80% des épis sont charbonnés alors que l'on ne trouve aucune attaque d'insectes.

Cette étude doit être considérée comme un essai préliminaire, des conclusions définitives ne pourront intervenir que lorsque nos connaissances sur l'ensemble des insectes nuisibles aux oasis sahariennes auront fait l'object de recherches plus méthodiques et plus approfondies.

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ROLE DES INSECTES SOCIAUX DANS LES TERRAINS DU SAHARA

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(Alger)

Introduction:

Au désert, les pâturages naturels, les cultures, les constructions humaines sont abondamment peuplés par les Fourmis et Termites du sol. Ils existent partout: un arbre isolé, une touffe de plantes rencontrée fort loin de tout autre végétal, abritent et nourrissent une ou plusieurs sociétés de ces Insects. Il n'est pas exagéré de dire que leur influence au Sahara, souvent très nuisible, est encore plus importante que sous les Tropiques. En effet, la rare végétation, particulièrement vulnérable après une longue période sèche, est facilement achevée par les Termites, ou quelquefois protégée par des Fourmis insectivores.

Cependant, la distribution, le comportement et même la systématique de ces animaux si communs étaient encore, en 1944, relativement peu étudiés. Depuis les voyages classiques de Forel (1898) et de Lameere (1901) en Algérie, seules quelques notes de Santschi (1910 à 1935) renseignent sur les Fourmis de Sud tunisien. Pour les Termites, la faune de Tripolitaine et du Fezzân était la moins mal connue, grâce aux travaux de Silvestri (1912 à 1924) et aux observations de Scortecci (1933 à 1939). En Egypte, au Moyen-Orient, en Asie Centrale, les investigations restent surtout taxonomiques, à part l'excellente monographie de Menozzi (1933) sur les Fourmis récoltées par Bodenheimer en Palestine.

Pendant et après la seconde guerre mondiale, les missions en Afrique se multiplient, mais peu comprennent des spécialistes d'Insectes sociaux. Signalons à cet égard la randonnée d'Alger au Cameroun, consacrée aux Termites, effectuée en 1948 par Grasse et ses collaborateurs. Les très intéressants résultats biologiques obtenus sur les formes sahariennes occidentales ne sont pas encore tous publiés. Dans la partie centrale du grand désert, grâce au Gouvernement Général de l'Algérie, j'ai pu observer et récolter Fourmis et Termites, durant 5 mois en tout (Bernard, missions au Fezzân (1944 et 1945) et au Tassili des Ajjer (1949)). Enfin, quelques localités du Nord du Sahara et des Hauts Plateaux furent explorés récemment par Pierre (Beni-Abbès, Erg occidental), par Hollande (Hauts Plateaux, Bou Saâda) et par moi-même (centre des Hauts Plateaux, sud tunisien).

Au total, une douzaine d'entomologistes ont examiné sur le terrain les espèces sociales du Sahara. C'est relativement peu, si l'on songe à l'étendue à parcourir et à la complexité des phénomènes à étudier. Toutefois, aujourd'hui, le rôle pratique et l'identité des types dominants peuvent être précisés. Bien qu'un dixiéme seulement du désert soit suffisamment connu, la répartition des formes les plus importantes est assez vaste pour que les résultats ci-dessous aient un degré satisfaisant de généralité.

Etat actuel des connaissances:

Les Guêpes et les Abeilles sociales sont pratiquement négligeables, en raison de leurs grands besoins d'eau et de fleurs. Même dans les oasis, l'Abeille domes-

tique est inconnue car elle ne trouverait aucune fleur durant les trois quarts de l'année. La seule Guêpe signalée est un Frelon: *Vespa orientalis*, banal en Asie chaude, plutôt rare au Sahara. Il n'est abondant que dans les vallées du Tassili n'Ajjer, massif exceptionnellement riche en sources et en lacs, où il est représenté par sa variété *Zavattarii*, de couleur brun-chocolat. Peu agressif, il se montre bienfaisant par les Insectes phytophages qu'il détruit. Les Touareg le nomment An'kokar.

En 1902, les myrmécologues ne citaient du Sahara que 25 espèces de Fourmis, surtout récoltées dans le Sud algérien. Leur nombre s'est élevé à 41 en 1940, à 66 actuellement. Mais 15 Fourmis seulement ont une importance réelle pour la vie des cultures et des sols. La plupart de ces Insectes communs, loin d'être des sahariens stricts, ont une large distribution dans le sud méditerranéen et l'Asie occidentale. Au contraire, dans l'ordre des Termites, habituellement très hygrophile, les types adaptés aux pays arides sont peu nombreux, et souvent nuls en régions humides. Leur classification est délicate, et nous évaluerons très provisoirement à 9 le stock d'espèces sahariennes connues, dont 2 seulement, très nuisibles, jouent un rôle économique capital dans l'ensemble du désert. Leur biologie ne commence à être élucidée que depuis 1948, et bien des points restent mystérieux.

Ces deux groupes montrent combien il faut être prudent pour les conclusions biogéographiques. Si les Fourmis sahariennes les mieux adaptées appartiennent à des genres tropicaux très évolués et récents (par exemple *Monomorium* et *Acantholepis*), par contre les Termites xérophiles dominants représentent des types archaïques, réfugiés dans les montagnes et les pays secs (Hodotermitidae et Psammotermitnae).

Les Termites:

Tous les Termites communs du Sahara rongent tiges, racines et bois de construction. *Aucune plante locale* n'échappe à leur atteinte, et même les Asclépiadacées les plus vénéneuses, comme le grand *Calotropis procera*, sont attaquées. J'ai revu au Fezzân un fait dèja observé par les chercheurs italiens: en plein reg dénudé, sans aucun végétal apparent, on trouve parfois des *Psammotermes* à quelques centimètresdans le sol. Ils subsistent là grâce aux troncs subfossiles de l'ancienne flore disparue après le pléistocène humide, notamment dans le bois des gros *Tamarix* recouverts par les alluvions des inondations passées.

Leurs dégats les plus manifestes concernent les troncs d'Acacias et de Palmiers, matériaux employés ici pour les habitations et le soutènement des puits. Au bout de 4 à 12 ans, les troncs de Dattiers qui renforcent la paroi des puits s'effondrent, entièrement minés par *Anacanthotermes*. Les poutres des maisons, particulièrement habitées par les *Psammotermes*, s'écroulent aussi, mais plus lentement. Le bordj militaire de Timimoun est ainsi entièrement à rebâtir. Moins apparentes, mais encore plus nocives pour l'avenir de l'homme au Sahara, sont les destructions opérées dans les pâturages naturels, loin des oasis. Les Termites mangent les tissus végétaux morts et altèrent peu les parties vivantes. Mais, après une suite de 4 ou 5 années sans pluies (cas fréquent au désert), les plantes spontanées. desséchées, sont achevées par les *Psammotermes*. Exemples: les pâturages à *Calligo-*

num comosum du sud du Fezzân en 1944, ceux du centre du Tassili n'Ajjer en 1949. Le Sahara occidental, à l'ouest du méridien d'Alger, ne paraît pas changer beaucoup de climat depuis 1900. Mais la partie orientale (Tunisie, Fezzân, Egypte etc.) est en aridité accrue, de l'avis de nombreux spécialistes. Beaucoup de points d'eau, abondants il y a 50 ans, sont maintenant à sec, et divers pâturages ont disparu. Cette évaporation semble corrélative du recul général des glaciers sur le globe, elle est, en tous cas, aggravée par l'action des Termites sur la flore.

Sur le comportement de chaque espèce je serai bref, car les observations plus complètes de la mission Grasse (1948) seront prochainement publiées. Il suffira de définir rapidement les principales différences écologiques notées:

Anacanthotermes ochraceus (Burm.) pullule dès les Hauts Plateau algériens et occupe tout le Sahara sauf sa lisière sud. Il remonte à plus de 2,000 mètres en montagne. Ce gros Insecte a encore des yeux chez les ouvriers et les soldats (ces derniers relativement rares). Les ouvriers, très fourrageurs, récoltent, en plus du bois, des morceaux de tiges de Graminées et des détritus végétaux. Chaque nid, très mal limité, est formé simplement de longues galeries, peu profondes dans le sol, pouvant dépasser 200 mètres de long. Aussi la reine est-elle très difficile à trouver: son premier et unique exemplaire connu a été capturé par Grasse en 1948. *Anacanthotermes ochraceus* préfère le sable et les rochers à l'argile, et supporte bien les terrains salés. Il manque souvent dans les pâturages à sable argileux éloignés des habitations, mais semble exister sans exception dans tous les oasis. Une espèce voisine: *A. Wasmanni* Sjöstedt, peuple surtout la bordure nord du désert et l'Atlas saharien. Ses sexués ailés sont noirs, et plus petits que les sexués jaunes d'*A. ochraceus*. La biologie est très analogue. Les *Psammotermes* sont des Termites de faible taille, aveugles, montrant un grand polymorphisme des soldats, très nombreux, dont la longueur varie du simple au double dans un même nid. Celui-ci est aussi ramifié et long que chez *Anacanthotermes*, mais pénétre plus profondément dans le sol. La mission Grasse a prouvé que depuis la termitière, située sur une dune, les Insects sont capables de descendre de 10 à 30 mètres jusqu'à la couche aquifère, d'où ils rapportent de l'eau dans leur bouche pour humecter les galeries. Nous verrons ci-dessous un comportement comparable chez la Fourmi *Acantholepis frauenfeldi.*

En plus du nid permanent souterrain, il y a parfois une construction externe, petite tour ou cube de 15 à 30 centimètres de haut. D'après les notes de Scortecci et les miennes au Tassili des Ajjer, cette tour existe surtout dans les lits d'oueds, et servirait aux *Psammotermes* à s'élever au-dessus des alluvions, trop humides et collants après les crues. En période sèche, ces habitacles saillants sont généralement abandonnés.

Géographiquement, *Psammotermes* est nettement plus méridional que le précédent genre: il manque au nord du parallèle de Ouargla, mais atteint par contre la savane sèche du Soudan. Il ne dépasse guère 1,3000mètres au Tassili, et n'est pas signalé dans l'Atlas. Mais, dans son domaine propre, il est très ubiquiste, commun dans les terrains argileux et les pâturages isolés où manque *Anacanthotermes.* Il attaque peu les Palmiers, mais surtout les Graminées, les *Calligonum,* les Acacias

et les *Tamarix.* Seuls les lieux trop salés lui sont défavorables, ainsi que les terrains à sable grossier. Une seule espèce parait valable: *P. hybostoma* Desneux. Mais une multitude de races géographiques compliquent son étude, comme d'ailleurs chez *A. ochraceus.* D'aprés une étude inédite de G. Richard (1952), les soi-disants 'ouvriers' de *Psammotermes* ne seraient que de jeunes sexués.

Un *Amitermes,* encore à l'étude, est parfois nuisible çà et là. Enfin, pour se limiter aux Termites communs, il y a au Sahara un Métatermitide sans Flagellés symbiotiques; c'est le petit *Microcerotermes* (forme principale: *M. eugnathus* Silv.). Il abonde sur les Hauts Plateaux et dans les pâturages du Nord, et se retrouve à Tamanrasset (Hoggar). Au sud de Colomb-Béchar, les plantes sauvages sont recouvertes d'épaisses croûtes de sable argileux par cet Insecte. Moeurs peu connues, dégâts moins importants que ceux des genres précédents.

Les Fourmis

Les premiers observateurs des espèces sahariennes: Forel et Lameere, ne pouvaient préciser le rôle économique des Fourmis locales, dont le régime alimentaire demeurait souvent inconnu. De plus, la région alors explorée (Autour de Biskra, Touggourt et Ghardaïa) ne représentait qu'une très faible fraction du désert.

Aujourd'hui, le comportement et la répartition des principaux types sont assez décrits pour que l'on puisse faire un bilan approximatif de l'équilibre entre Fourmis utiles et nuisibles. J'ai tenté d'évaluer cette concurrence sur les divers genres de terrain, selon la méthode des relevés quantitatifs: Dans un biotope aussi homogène que possible par le sol, la pente et la flore, on dénombre les fourmilières présentes. Après avoir trouvé une cinquantaine de nids, le pourcentage est établi pour chaque espèce. Un tel relevé rapide prend une heure ou deux, et c'est le seul procédé commode durant les courtes haltes des caravanes. Le résultat fournit une notion assez satisfaisante du peuplement, car chaque nid est l'unité biologique pour les Insectes sociaux. La plupart des formes ont des terriers très visibles sur le sol désertique, grâce aux déblais expulsés. Les inconvénients certains de cette méthode ont déjà été examinés dans notre travail de 1948 sur le Fezzân, et je n'y reviendrai pas ici.

Au total, 72 relevés semblables furent pratiqués jusqu'à présent au Sahara, de 0 à 1.800 mètres d'altitude, et de la latitude de Tozeur (sud-tunisien) à celle d'El Gatroûn (Fezzân sud-est). Les facies étudiés sont assez divers, et l'écologie de chaque Fourmis assez constante d'une région à l'autre, pour permettre les déductions suivantes:

(1) *Fourmis utiles et Fourmis nuisibles:* Les seules formes réellement insectivores (s'attaquant principalement aux Termites et aux Fourmis granivores *Messor*) appartiennent au genre *Cataglyphis* Förster. Ce sont de grandes Fourmis très agiles, souvent à reflets argentés, sortant jour et nuit et chassant isolément. Leurs 5 espèces sahariennes (3 très communes et 2 plus rares) peuvent être considérées comme bienfaisantes pour la végétation. Un peu plus omnivores, les petits *Acantholepis* (3 espèces) paraissent toutefois surtout mangeurs d'Insects, donc utiles.

A l'extrême opposé, 15 espèces environ, dont 3 abondantes partout, se montrent franchement nuisibles, soit en protégeant les Homoptères à miellée sur les plantes (*Tapinoma simrothi* Krausse, *Crematogaster oasium* Sant., *Paratrechina jaegerskjoeldi* Mayr etc.), soit en récoltant une bonne partie des graines locales (*Messor aegyptiaca* Em., *Monomorium chobauti* Em., et d'autres). Sur les Hauts Plateaux, on évalue que les *Messor* détournent 10 à 15% de la récolte de céréales.

Mais ces cas bien tranchés ne concernent que 23 Fourmis sur les 66 connues du désert. Les 43 autres, plus ou moins omnivores, compensent souvent, par les animaux phytophages qu'elles détruisent, leurs propres dégâts, directs ou indirects, à la végétation. En voici des exemples: *Monomorium salomonis* (L.) lèche rarement le miellat des Homoptères et capture divers insectes, mais certaines de ses races (surtout la sbsp. *didonis* Sant., très commune) ont une prépondérance de graines variées dans 50% des nids ou davantage. Ces lignées granivores sont observées aussi chez plusieurs *Pheidole* et *Tetramorium* de la région.

(2) *Influence du milieu sur le pourcentage de Fourmis utiles:* Le tableau écologique ci-dessous n'a pas besoin de longs commentaires pour établir l'effet du terrain sur la faune. Après divers essais de classement, les stations de rellevés se groupent, assez naturellement, comme suit: *En terrain sec* (sable pur, rochers, fortes pentes argileuses ou rocheuses) le rapport des fourmilières utiles à celles des espèces franchement nuisibles varie de 6 à 28. Les *Acantholepis* d'origine méditerranéenne (*A. frauenfeldi* Mayr., très répandu, *A. ajjer* Bernard, dominant au Tassili) jouent le rôle principal ici, sauf sur les rochers où *Monomorium salomonis* abonde. Dans plus des 9/10 du désert, pauvres en couches aquifères superficielles, il y a donc une forte majorité de Fourmis protégeant la flore contre les Termites. *Les terrains salés* occupent encore une vaste superficie dans les dépressions sahariennes. Les recherches au Fezzân montrent que le type de sels, variable d'un point à l'autre (chlorures, sulfates ou carbonates y dominent) a moins d'importance vis-à-vis des Fourmis qu'une propriété générale de ces substances: celle de retenir longtemps de l'eau. Sous la croûte salée, sèche et dure en surface, il y a généralement un sable jaune, contenant de 5 à 50% de sels. Ce milieu spécial est richement peuplé, mais la plupart des espèces nuisibles et des *Monomorium* le tolèrent mal. *Acantholepis frauenfeldi* réussit très bien là encore, et peut enrichir son nid en eau en remontant de la profondeur des boulettes salines humides, phénomène vu à Mourzouk (Fezzân) et à Beni-Abbès (Algérie occidentale) au cours de mes relevés numériques. Des formes hygrophiles des jardins, omnivores: *Camponotus maculatus* (Fab.) et *Pheidole pallidula* Nyl. s'ajoutent à cette faune. Les types utiles restent ici en majorité, sauf dans quelques palmeraies trop ombragées, où les *Cataglyphis* et *Acantholepis* ne trouvent pas la forte insolation qui leur est nécessaire.

La proportion des Fourmis nuisibles augmente beaucoup dans les *terrains aquifères peu salés* (fonds d'oueds, jardins arrosés ...). Cela tient à ce que les espèces utiles du désert, presque toutes xérophiles, résistent mal à l'inondation par les oueds ou à l'arrosage. Au contraire, les *Crematogaster* et surtout l'envahissant *Tapinoma simrothi*, genres d'origine tropicale, pullulent dans les jardins, où ils deviennent largement dominants. C'est encore plus vrai dans le Sahara du Nord et

TABLEAU ECOLOGIQUE DES PRINCIPALES FOURMIS SAHARIENNES

Sauf dans la première colonne, les terrains étudiés sont en pente faible ou nulle (0 à 15°). Chaque nombre donne le pourcentage moyen des nids de chaque espèce dans le peuplement, d'après 7 ou 8 relevés en des stations diverses du Sahara septentrional et central. Les 14 Fourmis les plus abondantes sont seules cités.

	Terrains arides			Terrains salés à plus de 5%			Terrains humides ou arrosés, peu salés		
	pentes $>40^o$	sable pur	rochers	incultes	cultivés et dénudés	ombragés	sable ± argileux inculte	cultures ensoleil-lées	cultures ombragées
I. UTILES	85%	60%	26%	63%	44%	38%	24%	11%	5%
Cataglyphis bicolor	0	0	0	15	16	7	1	4	2
C. albicans	10	1	15	16	4	6	13	2	0
C. bombycina	0	30	0	0	1	0	3	2	1
Acantholepis (3 esp.)	75	30	11	32	23	25	7	3	2
II. MIXTES	12%	34%	70%	33%	52%	45%	53%	69%	59%
Monomorium salomonis	11	35	48	9	2	15	23	14	9
M. gracillimum	0	0	0	3	5	7	1	27	13
Pheidole (3 esp.)	0	1	0	11	7	4	0.5	14	20
Camponotus maculatus	0	0	0	3	19	11	0	2	6
C. compressus	0	0	4	0	1	2	9	1	1
III. NUISIBLES	3%	6%	4%	4%	4%	17%	23%	20%	36%
Tapinoma simrothi	0	0	0	0	2	15	4	9	22
Messor (5 esp.)	0	0	0	4	0	1	7	10	2
Crematogaster (3 esp.)	3	2	4	0	2	1	9	1	0
Monomorium chobauti	0	4	0	0	0	0	3	0	12% (Paratrechina)
Rapport: utiles/nuisibles	28	10	6.5	16	11	2.2	1	0.5	0.17

l'Atlas, où *Tapinoma* sort des oasis et grouille sur les alluvions ensoleillés, de jour et de nuit, entretenant force Homoptères sur toutes les plantes.

En résumé, *Acantholepis frauenfeldi*, utile, et *Monomorium salomonis*, indifférent, sont de loin les 2 Fourmis dominantes, assurant souvent à elles seules plus de 60% des nids. Leur importance diminue dans les sols humides et peu salés, où les omnivores *Monomorium gracillimum* et *Pheidole*, les nuisibles *Messor, Crematogaster* et *Tapinoma* l'emportent.

Procédés de Défense:

La lutte directe contre les Termites sahariens semble inopérante, à cause de leurs galeries diffuses, longues de centaines de mètres et du prix élevé des insecticides efficaces. Sans pouvoir guérir les dégâts commis, mieux vaut prévenir de futurs accidents par les mêmes méthodes qu'en Afrique Noire: pas de bois dans les constructions, poteaux imprégnés de créosote, et surtout extirpation complète des racines et des bois souterrains autour des fondations d'un bâtiment et sous elles. Je renvoie sur ce point à la brochure de Grasse (Revue de Pathologie végétale de France, volume 23, 1936, fascicule 4).

La Fourmi la plus nuisible dans les oasis (*Tapinoma simrothi*) est passible des mêmes moyens de lutte que le fameux *Iridomyrmex* américain: appâts de sucre arsénié, placés dans des pots accrochés aux troncs d'arbres. Ce sucre à 2% d'arséniates empoisonne les reines et amène, au bout de quelques mois, l'extinction des fourmilières. Les *Crematogaster* et *Paratrechina* seront détruits en même temps.

Reste le problème, plus nouveau, de la protection des Fourmis utiles. Dans la plupart des pâturages à chameaux, elles se trouvent déjà en majorité. Autour des cultures, elles continuent à prospérer si le sol demeure salé. Il faut donc éviter qu'un arrosage excessif, ou des fuites des seguia (canalisations des oasis) viennent dessaler les emplacements incultes. Non seulement le sel favorise les nids des *Cataglyphis* et des *Acantholepis* aux dépens des *Tapinoma* et des *Messor*, mais encore la lumière solaire qu'il renvoie parait exciter le métabolisme et la chasse de ces insectivores rapides, les plus agiles des Fourmis africaines.

Résumé.

(1) L'importance économique des Termites et Fourmis paraît encore plus grande grande au désert que sous les Tropiques, car ils existent au pied de tous les végétaux, même les plus isolés, facilitant le déclin de ces plantes après une longue période sèche. Quelques Fourmis des genres *Cataglyphis* et *Acantholepis* protègent au contraire la flore en dévorant des Termites et des larves phytophages. On connait aujourd'hui 9 espèces de Termites au Sahara, dont 2 très nuisibles, et 66 Fourmis différentes, dont environ 8 manifestement utiles et 15 néfastes pour les cultures.

(2) L'écologie des 2 Termites dominants est résumée. *Psammotermes hybostoma* Desneux existe partout, et fait ses principaux dégâts dans les pâturages naturels et dans les maisons. *Anacanthotermes ochraceus* (Burm.) manque parfois dans les pâturages et les maisons, mais supporte mieux le sel et le sable grossier; il détruit notamment les constructions soutenues par des troncs de Palmiers.

(3) Un tableau de répartition quantitative des 14 Fourmis principales sur

divers types de terrains est donné. Généralement, les sols très arides ou très salés avantagent les espèces utiles. Les sols aquifères peu salés, surtout s'ils sont ombragés, favorisent les nuisibles, dont la plus commune est *Tapinoma simrothi* Krausse.

(4) Les méthodes de lutte contre les Termites seront essentiellement préventives (extirpation de tous bois ou racines autour des futures constructions humaines). Contre *Tapinoma* et formes analogues, les appâts sucrés empoisonnés sont recommandés. Enfin, il est possible de protéger les Fourmis utiles en évitant la dessalure des sols incultes entourant les jardins.

Références

Les références de presque tous les travaux cités se retrouveront dans 2 publications récentes de l'Institut de Recherches Sahariennes de l'Université d'Alger.

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Bernard, F. 1952. Les Fourmis du Tassili des Ajjer. *Série du Tassili*, 1, 105-190.

[*Ces volumes peuvent être obtenus en écrivant à l'Institut de Géographie de la Faculté des Lettres d'Alger, ou à la librairie Lechevalier, 12 Rue de Cournon, Paris (6e).*]

THE MICROBIOLOGICAL FORMATION OF SULPHUR IN CYRENAICAN LAKES

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The importance of sulphate-reducing bacteria (Type name: *Desulphovibrio desulphuricans*) in the formation of non-volcanic deposits of sulphur has been recognised by geologists and microbiologists for many years. It is thought that the organisms reduced sulphates to sulphides, which were then oxidised to sulphur by chemical or microbiological processes, or by a combination of both. Hunt (1915) attributed the formation of the Sicilian deposits to bacterial sulphate reduction in marine conditions similar to those existing in the Black Sea. Schneegans (1935) discussed the function of sulphate reducers in the formation of some French deposits. The great Texas and Louisiana deposits are said to be the result of microbiological sulphate reduction (ZoBell, 1936), though the evidence is necessarily speculative. More direct evidence was obtained by Subba Rao, Iya & Sreenivasaya (1947) and Subba Rao (1951). They attributed the formation of the sulphur in sulphur-bearing clays (27-35% sulphur) in certain coastal areas of India to the catalytic oxidation of sulphide by atmospheric oxygen in the presence of iron. They conducted field trials using cultures of sulphate reducers isolated from the sulphur-containing clay, and demonstrated the formation of sulphur in near-natural conditions. Murzaev (1950) discussed the microbiological production of free sulphur in the muds of Russian lakes and suggested experiments to stimulate its formation.

Mancuso (1939) studied the geochemistry of an area in the Libyan desert south and west of El Agheila characterized by salt marshes and many small saline lakes. He described one lake, Ain-el-Braghi, in some detail; it differed from the other lakes examined by him in being fed by a warm sulphur spring (32-34°C). He noted the abundant escape of hydrogen sulphide, which he attributed to the reduction of calcium sulphate by 'sulphur bacteria'. Some of the hydrogen sulphide was oxidised to finely-divided sulphur which gave the lake a characteristic milky-white appearance. The sulphur slowly settled on the bottom to form a deposit.

In January 1950 we received a report by Pinfold & Gee (1949) on sulphur-producing lakes about 20 miles south west of El Agheila. It seemed probable that a detailed examination of these lakes would be of scientific interest from the point of view of the processes involved in the formation of natural sulphur deposits, and might give information and cultures useful in working out an industrial process for sulphur production. We visited the area in May 1950 and examined four lakes (*Chemistry Research 1950,*). 1951).

The Sulphur-Producing Lakes

The four lakes examined were: (1) Ain-ez-Zauia, (2) Ain-el-Braghi, (3) Ain-el-Rabaia, (4) Ain-umm-el-Gelud.

These lakes lie in a stretch of salt marsh running for about 30 miles in a S.E. direction from a point 30 miles W. of El Agheila, which is in the S.E. corner of the Gulf of Sirte 200 miles S.W. of Benghazi. We camped near Ain-ez-Zauia for two

nights. The other three lakes were visited all on one day and received only a cursory examination.

General Description of Ain-ez-Zauia. The lake, reputed to be the most productive in the area, lay 20 miles S.W. of El Agheila in a long narrow salt plain. There were two pools of unequal size connected by a swiftly flowing stream (Fig. 1). The lake was supplied by a warm spring rising in the smaller section, for water of temperature 30-32°C (shade temperature 16°C) flowed out of it in two streams, one into a mass

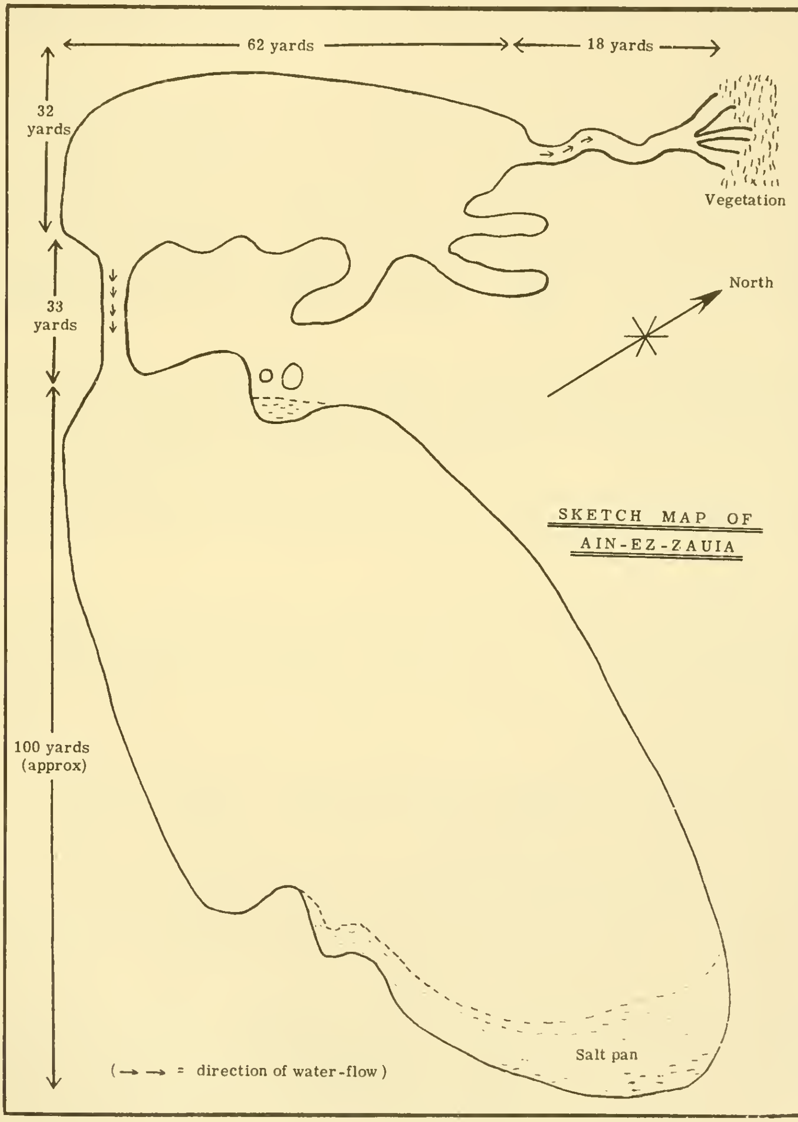

Figure 1.
Sketch map of Ain-ez-Zauia

of vegetation in the salt plain, the other into the larger section. In brilliant sunshine (on May 3rd-4th, 1950), the main body of water reflected a vivid milky blue, though a bottle sample was virtually colourless with a slight haze. The blue of the smaller section was deeper and more vivid than that of the larger, probably owing to a greater concentration of suspended particles of colloidal sulphur. Bordering the blue was an uneven band of red gelatinous material, stretching in some places several yards from the banks in shallow water. Bulbous formations (4" × 2") could be seen in this red material and a few red masses were floating in the water. There was a pronounced smell of hydrogen sulphide and some wind-blown sulphur was visible near the banks. Salts were crystallising out round the edges of the lake.

Other observers have given descriptions differing from ours in important details. Pinfold and Gee, who visited Ain-ez-Zauia on October 7th, 1949, made no mention of the red material bordering the pools, but reported numerous floating masses of a red jelly-like material. It is remarkable, too, that Mancuso, who saw Ain-el-Braghi several times in 1937, makes no mention of the red material, and describes the water as milky-*white*; when visited by us on 6th May, 1950, it showed the same colour characteristics as Ain-ez-Zauia. Clearly the appearance varied considerably with the season and with the observer.

Detailed Examination of Ain-ez-Zauia. We carried a specially designed 'desert laboratory' which contained sample bottles, apparatus for sampling water from different depths and bottom mud, solutions and apparatus for sulphide and pH determinations and an alcohol lamp. Samples from different parts of the lake were taken from an inflated rubber dinghy. Most of the samples were stored for future examination at Teddington; others were examined microscopically beside the lake. The principal results of the examination are given below.

(1) *General.* The water was saline and had a pH of 7.4. Its probable composition is given in Table 1. Noteworthy points are the presence of about 2% NaCl and of a saturated solution of calcium sulphate, the latter derived from crystalline gypsum, lumps of which could be detached from the bed of the lake. The presence of boron was also mentioned by Mancuso. The organic content is low.

(2) *Sulphide formation.* The evolution of hydrogen sulphide was strong evidence for the activities of sulphate-reducing bacteria. The concentration of sulphide in bottom water samples was 108mg. H_2S/1., and at the surface 15-20mg. H_2S/1. Microscopical examination showed that many vibrios resembling sulphate reducers were present. Enrichment cultures of these organisms were subsequently obtained from practically all water and mud samples, from which several pure strains were isolated. Two of these strains were found to be unusual, in our experience, in being unable to utilise gaseous hydrogen for sulphate reduction, i.e. they contained no hydrogenase enzyme (Adams *et al.*, 1951). It seems reasonably certain on this evidence that sulphate reduction by sulphate-reducing organisms was taking place in the lake. It is possible, however, that some H_2S entered with the warm spring supplying the lake.

(3) *The Coloured Gelatinous Material.* This carpet-like material developed prolifically in the shallow waters, in places stretching several yards from the banks and sometimes appearing above the water level. It was composed of gelatinous mater-

TABLE 1

Probable Composition of Water from Ain-ez-Zauia

	Parts per million
Calcium bicarbonate, as $CaCO_3$	237
Calcium sulphate, as $CaSO_4$	2,613
Calcium chloride, as $CaCl_2$	880
Magnesium chloride, as $MgCl_2$	1,325
Ammonium chloride, as NH_4Cl	24
Sodium chloride, as NaCl	19,290
Potassium chloride, as KCl	630
Potassium nitrate, as KNO_3	5
Silica as SiO_2	70
	25,074
Total solids	25,250
Organic matter, traces of phosphate and borate	176
pH	ca. 7.3
H_2S	see text
Suspended solids ($CaSO_4$, SiO_2 and S)	2,816 p.p.m.
Phosphorus, as P_2O_5	1.1 p.p.m.
Boron, as B	5 p.p.m.

ial, red on the surface but with green and black matter underneath. In places it was about ½" thick. When pierced, the carpet released occluded gas. Microscopical examination at the lake side showed that it contained many sulphur granules, crystals (?$CaSO_4$), many spiral bodies and a few protozoa; but the bulk of the material was an amorphous mass of cellular material and sulphur granules. It was later recognised as coloured photosynthetic sulphide-oxidising bacteria: *Chromatium* (red bacteria storing sulphur granules *inside* the cell) and *Chlorobium* (green bacteria which precipitate sulphur *outside* the cell). These organisms require light for growth; hence their massive development in the shallow water only. They were also detected in mud taken from the deepest part of the lake (about 9 ft.) and in surface water samples.

Subsequently, pure cultures of both *Chromatium* and *Chlorobium* were isolated using the techniques described by van Niel (1931). Old cultures of these organisms

formed zoogleal masses closely resembling the gelatinous material of the lake. It is therefore reasonable to conclude that the latter consisted chiefly of masses of the two photosynthetic sulphide-oxidising organisms. Both are obligate anaerobes. Their significance in the production of sulphur in sulphide-containing waters, which are essentially anaerobic, is discussed below.

(4) *Microbial Population.* In addition to the bacteria mentioned above and despite the anaerobic environment, aerobic organisms were present in the lake, predominantly at the surface (Table 2). Fourteen morphologically distinct types of aerobe, including a fungus, were isolated from the gelatinous material. Eight types were isolated from a bottom sample (9 ft.) of water, three from half way and four from a surface sample.

TABLE 2

Population of aerobic bacteria in samples from Ain-ez-Zauia

Samples of water from the middle of the lake were plated out on nutrient agar and the number of colonies recorded. Since there was a delay due to the journey to England, the figures probably do not represent the true natural population.

Depth	Count (colonies/ml.)
Surface	181,000
half-depth (*ca* 1.5 m.)	52,000
bottom (*ca* 3 m.)	57

Thiobacillus thiooxidans, an aerobic sulphur-oxidising organism, was not detected in water and mud samples, but it was present in samples taken above water level. *Thiobacillus thioparus* was only sought in the gelatinous material and was not found. Cellulose-decomposing bacteria were found only in one bottom mud sample, so were probably not plentiful. No algae were isolated with the exception of a blue-green alga from another lake, Ain-el-Braghi. These *Mycophyceae* are often observed in sulphide-containing waters (Allen, 1952).

(5) *Fish.* Despite the high concentration of salts and sulphide, shoals of small fish (1" - 2" long) were observed in the two streams leaving the smaller section of the lake. They were later identified as belonging to the genus *Cyprinodon*, (Smith, 1952). Mancuso (1939) reports that Desio (1935) collected *Cyprinodon* from Ain-el-Braghi in 1930.

(6) *Sulphur.* The vivid milky-blue appearance of the water by reflected light was undoubtedly due to suspended colloidal sulphur particles, which could be seen as highly refractive bodies under the microscope. A deposit of finely divided sulphur, 6" or more in depth, covered the bottom of the lake. This was removed annually by local Arabs. The possible processes responsible for this sulphur formation are discussed below.

(7) *Examination of Other Lakes.* Ain-el-Rabaia (roughly circular, 100 yards diameter) and Ain-el-Braghi (80 × 50 yards) were similar to Ain-ez-Zauia in smell (H_2S), colour (milky blue with coloured gelatinous material stretching 2-3 yards from the banks) and in producing sulphur. Both were fed by warm springs, but we were unable to take the temperatures because both our thermometers were broken. According to Mancuso, the temperature of Ain-el-Braghi varies between 32° and 34°C during the year. Ain-el-Rabaia appeared to be cooler.

Ain-umm-el-Gelud was considerably larger (approx. 1 × ½ mile) and was different in two important respects. It contained very little free sulphur, though there was a pronounced smell of hydrogen sulphide. There was also none of the coloured gelatinous material round its borders, i.e. there had been no mass development of sulphide-oxidising bacteria. It appeared likely that the non-production of sulphur was related to the absence of gelatinous material.

Sulphate-reducing bacteria and sulphide-oxidisers were isolated from all three lakes.

(8) *Recovery of Sulphur.* In the dry season the sulphur is scooped out by hand dredges made of sacking into shallow earthen pans at the water edge. The sulphur is left to drain and dry for a week. It is afterwards transferred to higher ground for further drying and is then collected into heaps for transport by lorry. The crude product contains about 50% sulphur, most of the remainder being sodium chloride (20%) and silica (12%). The total quantity recovered annually from three lakes is about 200 tons; the total amount formed would be larger.

Laboratory Experiments

Our observations in Cyrenaica suggested strongly that the formation of sulphur in the lakes was a microbiological process in which sulphate-reducing bacteria were associated with the coloured gelatinous material developing so prolifically in the shallow waters. We tested this hypothesis by experiments in an 'artificial lake'.

'Artificial Lake' Experiment. A 40-litre tank containing 'artificial lake medium' (Table 1 supplemented with sodium lactate as organic source) was inoculated with both the coloured gelatinous material and crude cultures of sulphate reducers from Ain-ez-Zauia. The whole was incubated at 32°C with continuous illumination from a 200-watt bulb 18" above the water surface. At intervals the sulphide concentration was renewed with saturated H_2S-water. The pH was maintained at about 7.5. After 5 days a red colouration appeared and sulphur deposition began. After a month a thick layer of gelatinous material containing sulphur covered the bottom of the tank, closely resembling that taken from the lake.

This experiment and others like it showed that sulphur formation could be induced in an artificial lake medium (with sulphate as the sole sulphur source) by inoculating with crude cultures of sulphate reducers and gelatinous material from the lake. Microscopical and bacteriological examination of the gelatinous material had shown that it consisted chiefly of the coloured photosynthetic sulphide-oxidising bacteria *Chromatium* and *Chlorobium.* It was therefore very probable that sulphur formation in the

lakes was at least partly due to the combined action of two groups of micro-organisms-(1) sulphate-reducing bacteria, which reduced the sulphate in the lake water to sulphide, and (2) photosynthetic sulphide-oxidising bacteria which oxidised the sulphide produced in (1) to elemental sulphur.

Experiments with pure cultures. Experiments with crude cultures cannot be accepted as proof that specific organisms are responsible for what occurs. For final confirmation of the hypothesis, experiments were carried out with pure cultures of sulphate reducers and of *Chromatium* and *Chlorobium*. All cultures originated from the lakes.

Mixed pure cultures of *D. desulphuricans* + *Chromatium* and of *D. desulphuricans* + *Chlorobium* were prepared in various media, based on combinations of the media used for the separate growth of the organisms and the composition of the lake water. The cultures were incubated anaerobically at 32°C in an illuminated cabinet. No source of sulphur other than sulphate was used. Growth of both pairs of bacteria occurred in nearly all cultures. Those containing *Chlorobium* and sulphate reducers deposited a yellow layer of sulphur (Fig. 2). No such layer appeared in the *Chromatium* cultures, but under the microscope the *Chromatium* cells were seen to be almost completely filled with sulphur globules. The best yield of sulphur (judged by inspection) was obtained from *D. desulphuricans* + *Chlorobium* grown in the medium in Table 3.

These experiments show that elemental sulphur can be produced from sulphate by the combined action of pure cultures of sulphate reducers and the photosynthetic green and red sulphide oxidisers in a common medium. They provide evidence that some of the sulphur in the Cyrenaican lakes was produced by a similar combination of sulphate reducers and *Chlorobium*.

Reducing agent for sulphate reduction. The reduction of sulphate by *D. desulphuricans* requires a reducing agent, either hydrogen or an organic compound such as lactic acid. The source of reducing agent for sulphate reduction in Ain-ez-Zauia was not clear since the organic content of the water was low (see Table 1), though the possibility exists that the continuous supply of this organic material by the spring was used for reduction. It was also possible that the coloured sulphide-oxidising bacteria, which can satisfy their carbon requirements by photosynthesis from CO_2, provided suitable organic matter for the sulphate reducers. To test this, mixed pure cultures of *D. desulphuricans* + *Chromatium* and of *D. desulphuricans* + *Chlorobium* were prepared with no carbon source other than $NaHCO_3$, and incubated in light at 30°C. In order to avoid false results due to carry-over of organic material in the inocula, the mixed populations were sub-cultured at least three times. At each stage they were inspected for sulphate reducers microscopically. In both cases the coloured sulphide oxidisers grew readily, and at each stage sulphate reducers were detected microscopically. The sulphate reducers were more plentiful in symbiosis with *Chromatium*, and if thiosulphate was used in place of sulphide as a sulphur source their presence could be detected chemically by blackening (FeS) after addition of a ferrous salt.

Figure 2.
Formation of sulphur from sulphate by the combined action of pure cultures of sulphate-reducing bacteria (*D. desulphuricans*) and sulphide-oxidising bacteria (*Chlorobium*).

TABLE 3

Medium for microbiological sulphur formation from sulphate

D. desulphuricans (Strain El Agheila Z) + *Chlorobium* sp. were grown in light at 30°C

	g./litre distilled water
Na_2SO_4	3
Na hydrogen malate	1
NH_4Cl	1
KH_2PO_4	1
$MgCl_2.6H_2O$	0.5
$CaCl_2$	0.1
NaCl	10
$NaHCO_3$	2
Yeast extract (Difco)	1

Trace element solution, 1 ml.; pH 7.3

The trace element solution contained the elements below:

	mg./litre
Fe as $FeCl_3.6H_2O$	500
B as H_3BO_3	100
Zn as $ZnSO_4.7H_2O$	100
Co as $Co(NO_3)_26H_2O$	50
Cu as $CuSO_4.5H_2O$	5
Mn as $MnCl_2.4H_2O$	5

Discussion

The available evidence suggests that the formation of sulphide in Ain-ez-Zauia and in the other three lakes examined was most probably due to bacterial reduction of sulphate. Sulphate reduction may also have occurred in the springs supplying the lakes. There are at least five processes by which this sulphide could be oxidised to sulphur.

(1) Atmospheric oxidation, which occurs in all sulphate-containing waters exposed to air, was undoubtedly responsible for some of the sulphur formed in Ain-ez-Zauia, but is too slow to account for the high sulphur yield. For example, Ain-umm-el-Gelud produced hydrogen sulphide but formed very little sulphur though it was exposed to atmospheric oxidation.

(2) Oxidation by nitrite formed by bacterial nitrate reduction (Iya & Screenivasaya 1944,) may have occurred, but the low nitrate content of the water would not favour it.

(3) Oxidation by *Th. thioparus*, which is an obligate aerobe, could have yielded sulphur at the air-water interface, but would not have occurred at lower (anaerobic) levels. Senez (1951) attributed sulphur formation in air by impure cultures of *D. desulphuricans* to this organism. *Th. thioparus* was not found in the samples examined for its presence, but it is a fragile organism and may not have survived the journey to England.

(4) Oxidation by *Chromatium* undoubtedly occurred in the lakes and was reproduced with pure cultures. However, *Chromatium* stores sulphur granules inside the cell and would therefore not produce free sulphur unless lysis of the cell occurred.

(5) Oxidation by *Chlorobium* also occurred and was demonstrated with pure cultures. As *Chlorobium* deposits sulphur outside the cell, oxidation by this organism could account for much of the sulphur formed in the lakes.

The importance of *Chromatium* and *Chlorobium* in sulphur formation is supported by three facts :-

(i) The insignificant production of sulphur in Ain-umm-el-Gelud corresponded with an absence of the coloured gelatinous material. This suggests that the coloured material, which consisted largely of *Chlorobium* and *Chromatium*, played a key part in sulphur formation.

(ii) *Chlorobium* and *Chromatium* are obligate anaerobes and, subject to light being available, would be active throughout the lake water. Aerobic sulphide oxidisers could only function at the surface.

(iii) *Chlorobium* and *Chromatium* synthesised organic matter from CO_2 and sunlight which would support growth and sulphate reduction by *D. desulphuricans*.

Thus there was probably a symbiosis between *D. desulphuricans* and the coloured sulphide oxidisers, in which the sulphate reducers formed sulphide for growth of the sulphide oxidisers, which in turn made organic matter photosynthetically for the sulphate reducers.

The formation of sulphur by this symbiosis is of considerable intrinsic scientific interest. It also suggests that the larger sulphur deposits in nature may have been laid down by a similar process. Its economic aspects are mostly obvious. No lakes other than those in Cyrenaica are known to produce sulphur on a scale sufficient to justify commercial exploitation. The production of about 200 tons annually is insignificant in relation to the prevailing shortage of sulphur. Nevertheless it suggests a method of augmenting sulphur supplies. Sufficient is now known of the physiology of sulphate-reducing bacteria and the coloured sulphide-oxidising organisms to make it clear that conditions in Ain-ez-Zauia are by no means optimal for the separate activities of these bacteria, though much more research is required before the best conditions for their symbiosis and for maximum sulphur production are established. Even so, it is possible that the addition of organic matter (e.g. vegetable waste) and phosphate might increase the yield of sulphur. Unproductive lakes such as Ain-umm-el-Gelud might be made productive by addition of necessary nutrients, which may be simple. More-

over, warm artesian springs containing sulphide and sulphate, and lakes in sunny climates might be induced to produce sulphur.

Present methods of harvesting the sulphur in the Cyrenaican lakes are very primitive and give an impure product. The yield would be improved by better extraction procedures, if it were economically feasible to use machinery in so remote an area. The sulphur yield alone would probably not justify such an enterprise, but combined with exploitation of the carnallite deposits at Marada, some 30 miles to the south, a viable industry might be developed.

Summary **Summary**

The continuous deposition of sulphur in certain Cyrenaican lakes is attributed mainly to the combined action of (1) sulphate-reducing bacteria, and (2) photosynthetic sulphide-oxidising bacteria (*Chlorobium* and *Chromatium*). In laboratory experiments, the latter synthesized organic matter for bacterial growth and sulphate reduction.

Some natural sulphur deposits may have been laid down by a similar process. Sulphur production might be stimulated or induced in other lakes.

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FORESTS, ARIDITY AND DESERTS.

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The Man-made desert is a stern reality which so far has rarely been faced up to. Man has been the enemy of the forest and of vegetation ever since he learnt to grow crops for food and to pasture flocks and herds on the countryside. The term erosion is widely used but very often without a real understanding of what is meant. It is easy for the public to understand one type when they see a raging torrent tearing out the heart of a hillside. But there are several different types of erosion which in the end may result in the same catastrophe, namely the production of desert or arid conditions, the methods being different.

I propose to confine myself here to one of the commonest and probably the oldest of the types resulting purely from the acts of man. The most ancient type of cultivation known to man is in nature and mainly covered with forest, being known in English by the name of shifting cultivation. This type of cultivation from its very origin has many different names, even in the one country. For example in India there was a different name for it in N. India, the Central Provinces, Bengal, Assam, Madras, Burma and Ceylon. In Europe in olden times the same variation in nomenclature existed. But the method was normally the same. A small piece of forest out of the surrounding mass was felled, the material as soon as dry enough fired, and the ashes roughly spread over the ground thus opened out and the seed of a crop sown. At the end of a few years, roughly three to five, a dense weed growth supervened, or the soil decreased in fertility, or both. The shifting cultivator then moved and repeated the operation in another piece of the forest. When the world was young and the population small the forest was the enemy and to obtain pasturage for increasing flocks the forest was fired to get rid of it. It was the increase in population that gradually and imperceptibly had its effect on the forest. In the temperate parts of the world and especially in the case of the conifers, great forests were swept away. In the tropical and sub-tropical forests, however, where the forests consisted of broad-leaved trees of many species intermixed, the forest did not necessarily disappear but suffered a slow degradation. Valuable timber species susceptible to fire disappeared but the forest remained. The habit of setting fire to the felled material on the area to be cultivated resulted in other fires spreading into the surrounding forest and the countryside during the hot season. This danger and damage is only too well known to the modern day forester. The eventual degradation of the forest from a fine dense high forest to a scrub, variously denoted scrub, bush or savannah, took thousands of years and was in effect so imperceptible that it had passed unperceived – in fact was lost in the past histories of the earlier nations who lived in what are now deserts. Wars helped in this disappearance with the habit of a retreating army of setting fire to the countryside to prevent pursuit. Sites of these old time nations are known to us. It is suggested here that it was this degradation of the forests and the drying up of the water supplies which led, in more than one instance, to the final disappearance of the peoples. Time does not allow me to mention such instances. In many parts of the world the shifting cultivator was therefore, to a certain extent nomadic. In

early times it was unnecessary for him to return to the piece of forest he had previously cut down. In later times he returned but only after the lapse of a century or more when a forest of second growth species had grown up. It was the increase in population and the disappearance of so much forest which resulted in the shortening of this period of return.

In British West Africa this method of cultivation is termed farming and the system is more fixed, since the people are under the rule of numbers of Chiefs, each having a fixed area of country with fixed villages under his jurisdiction. In British and French West Africa between the sea and the southern Sahara and including East Africa and the Sudan, this method of cultivation is in force over great areas of the so-called bush or savannah where the forest, for it is still forest though much degraded, is considered still to be good if it has a height of 30-40 feet and a corresponding density. The serious trouble is that the populations have greatly increased and with them the grazing and pasturing herds. But the area of land under a Chief and his people remains a constant. This results in a shortening of the fallow period and with a consequent more open and shorter scrub growth which produces less ash at the burning and a poorer crop. But more serious, an interference with the water supplies commences to make itself felt. This may be summarised as follows:-

(a) In the past the population of the regions now deserts, or on the way to become deserts, was very small. The slow depreciation of the soil conditions caused by a wasteful utilisation took many centuries to make its appearance. As is known, the nomadic tribes moved away from an area becoming unproductive to return to it, perhaps many years later, when it had recuperated. It was the earliest form of 'crop rotation' or more correctly 'grazing rotation'.

(b) With the increase in populations and in consequence in the intensity of the misuse of the soil the migration from an exhausted area was not followed, on any scale by a return at a later date. For those later migrations of more numerous populations were not apparently undertaken till the water supplies had become so unreliable and the soils so poor that neither the one nor the other were capable of supporting them.

(c) The decrease in rainfall supplies in springs, streams, rivers and wells precedes the decrease in the rainfall. Here apparently lies one of the greatest stumbling blocks to an appreciation in Africa of what is taking place under the misuse of the soils in the upsetting of the balance of nature. The rainfall becomes unreliable or intermittent.

(d) In the past this stage probably continued through the lapse of many centuries. The fluctuations waxed and waned over long periods. Later generations took the fitful rainfall as something which had now become a climatic reality which had to be put up with. Generations of people lived and died under these conditions as they are doing today. Travellers studying the land and its people, being misled by this fitfulness or intermittancy, reported that in parts the rainfall was improving and with this improvement the ground was becoming re-

covered with a vegetation after man had migrated from the area, or that records together with the statements of local villagers showed that the intermittent rainfall was due really to climatic oscillations over which man had no control.

(e) This in spite of the more modern evidence upon the ground that the populations – greatly swollen in numbers – were destroying the soil factors at an enhanced rate, and that the rainfall fluctuations were of greater intensity; that no one, scientist or African peasant, could predict the amounts of rainfall which would occur in the year, or the times at which within certain periods, it would fall. From the practical viewpoint of the administrator these are the points upon which clarification is required and upon which concentration would appear necessary.

Desiccation is a much debated term in Africa and elsewhere in the world. It is held to be due primarily to the over-utilisation of the vegetation covering of the soil under which productivity is reduced, the decrease of water supplies in the springs, streams, rivers and wells, the sinking of the water table in the soil strata, and decreases in the rainfall. It may be due to (a) the presence of neighbouring deserts and sand penetration; (b) erosion in varying forms through over utilisation of the soil; (c) a combination of (a) and (b), accompanied usually by dry hot or cold winds.

Lavauden (*Les Forêts du Sahara*) does not use the word 'climate' in connection with the process which he terms *déssèchment*, by this meaning only the progressive diminution of surface and subterranean water supplies. He does not discuss the relations existing between dis-afforestation and desiccation. Kennedy Shaw in considering this matter for Southern Libya says it is one of the present day increase of desert conditions due entirely or largely to the acts of man'. In northern Nigeria desiccation to whatever agency or series of agencies it may be subjected, is an accepted fact. Here it may, it is suggested, be attributed to a combination of erosion *sur place* (for the more level country) coupled with the lowering of the water table in the soil, the falling off of the rainfall, and sand penetration from the Sahara.

In some parts of Africa desiccation aided by sand penetration, may be due, in part, to blown sand from drying off river banks or diminishing lakes.

What is drought? An ordinary definition of 'drought' in the English language would refer to months of dryness at periods when the ordinary average rainfall is received. In Europe so far as records go, there appear to be years of wetter months followed by years of drier ones, and we speak of 'drought' in its true sense – more or less temporary climatic changes over which man can have little control. Can the word be equally applied, or applied with its true significance, to the upsetting by man of Nature's balance between the soil and its covering and the water supplies, with the resulting dislocation in the regular average water supplies received in the rainfall and from springs, streams, rivers and wells of the region? So far as we have knowledge and evidence of the results attendent upon this intervention of man in Nature's balance it is becoming more and more evident that periods of so-called drought will not be followed by consistent wet periods, as has been sanguinely hoped in some quarters in connection with the major catastrophes facing man in certain parts of the world. Such hopes are illusory. However the following proposition may be enunciated:- As a result of

erosion in one of its forms, water supplies have decreased either in moisture in the upper layers of the soil owing to the lowering of the water table, thereby, affecting wells; or decrease in, or cessation of, springs; or disappearance of the water in streams during the dry months of the year and lowering of the water level during the same period in the smaller and larger rivers. The rainfall has also decreased in annual amounts, though the amounts of such decrease may be slower in making their appearance; but, more alarming, this rainfall has become capriciously intermittent in its supplies – no man being able to forecast the amounts which will be obtained within the year; or often, within limits, at what periods.

This is not 'drought' in the ordinary accepted sense of that word. I would term it the 'Intermittent Stage' in rainfall supplies. It may be suggested that if the fact of the intermittency of the rainfall, developing at a certain stage in the degradation of the soil and its covering, be accepted as a factor of importance in this decrease in fertility, we can start from a point at which we all are voicing the same position of affairs and can commence, according to the different types of erosion, the business of combating the danger. Lavauden (*Les Forêts du Sahara*) wrote 'In the middle of the Quaternary period, an epoch which it is impossible to date precisely, the Sahara was a very humid region, the fluvial system was of a particularly powerful type, allied without doubt to very abundant precipitations. Today all these river beds are dry, and only the largest retain underground water of which the amounts constantly diminish – slowly perhaps but inevitably – owing to the *equilibrium existing between the precipitation and evaporation.* An important question is to determine at what epoch the dis-equilibrium between the two commenced to make itself felt; in other words at what period desiccation commenced to become seriously apparent.' This represents exactly what I term 'Intermittent Rainfall'.

It may be asked 'How can this stage be recognised on the ground?' Examples are only too plentiful. If we examine the regions bordering the southern edge of the Western Sahara (British and French colonies) it will be found that a stage is reached in the rainfall conditions where dependence upon them for crop production can no longer be placed with ordinary confidence. For certain localities in Northern Nigeria and the French Niger Colony the local population complain of violent winds which, blowing at the beginning of the rainy season about May or June, bring blown sand on to their fields. The millet crop is sown during the first rains. Should the previously normal second rains arrive up to time, when the seedlings have shown above ground the roots of the latter fix the sandy soil (it will be noted that there is already a sandy covering blown from the adjacent Sahara Desert covering the normal soil surface) and the growth of the crop proceeds successfully. Should the second and main rains not come up to time, however, sand carried by the strong winds covers the seedlings and kills them. The operation of sowing has then to be undertaken a second time and, maybe, a third or fourth. Indeed cases are on record when the seed has been sown as many as ten times! This example would appear to be a strong argument in favour of the postulate here advocated that a time arrives when the rainfall becomes intermittent and man can count no further on its reliability.

It has become apparent that in some quarters opinions are held that there can be no analogies between, say, the desiccation being produced in parts of Africa and the

conditions under which the Dust Bowls have arisen in America or the soil drift taking place in Southern Australia. If, however, we trace all categories of erosion back to their origin or commencement it is possible to show in most cases that in this over utilisation of the resources available, with the consequent upsetting of Nature's balance, a stage was, with few exceptions, always reached at which the factor which governs all production and life, the water supplies, commenced to become intermittent. One way or the other this stage must have made its appearance.

Under excessive utilisation of the soil then, the rainfall supplies in the region fall into a delicate stage of oscillation,. It has been mentioned above that the first decreases noticeable to man in the local water supplies show themselves in a lowering of the water table in the soil owing to a decrease in the water in springs or their 'drying up', including the wells, the drying up of streams in the hot months of the year, and the lowering of water levels in the rivers. These partially precede the 'falling off' in the rainfall supplies. Man's life is short, his official service life shorter still, these gradual manifestations occur almost imperceptably, though the speed is now-a-days much accelerated, and long periods have passed before the balance delicately dropped on the wrong side and man's chance of repairing the damage done is gone – for the desert or conditions of aridity have won.

What of the present day? The world has been shocked at the appaling conditions which have been produced in the Dust Bowls in the United States and Canada in a brief half century of over-utilisation of the soil assisted by all modern developments. And yet whether it is a result of fifty years or thousands of centuries the outcome is the same and the dangers are the same whether it be on the southern edge of the Sahara where sand penetration assists desiccation, the Creeping Desert in the Sudan, the level country at the foot of rapidly eroding hill ranges, the periphery of the Dust Bowls in America, or the confines of the soil drifts forming desert in Australia; and also the danger to the neighbouring agricultural or pastoral country is the same, namely the extension of the existing destroyed regions over their boundaries owing to gradual further desiccation, dust storms and so forth. It is in these neighbouring lands that the intermittent rainfall stage has been reached and man is called upon to make his effort to restore the balance of aforetime before it is too late.

Mr William Vogt is well known as the author of *Road to Survival.* He is a member of the Chief Conservation Section of the United States Forest Service and has spent nine years studying forests and forestry conditions in South America. He prepared a memorandum for a Sub-Committee of the Forestry Section of F.A.O. which met in Geneva in August 1947. His memorandum showed that against generally accepted opinions amongst foresters, the Latin American Republics do not hold the enormous forestry resources they were supposed to. He bases his reasons on the physical geography of Latin America and the pattern of human settlement. The tropical lowlands are not desirable for human settlement owing to prevalent diseases; also a high proportion of the area is unsuitable for agriculture because of excessively concentrated rains that leach minerals from the soil, long blistering dry seasons that thoroughly desiccate the vegetation once the forest has been cleared. and because high temperatures tend to oxidise very rapidly organic materials in the soils. It is not at all un-

usual for a tract of land to pass from virgin forest to abandoned bush, when the low-lands are cultivated, within a period of eight or ten years.

Dealing with the coffee and tea planter in Ceylon and Madras, Colonel Beddowe, Conservator of Forests, Madras, wrote in 1876 'It must not be supposed that coffee is at all a permanent cultivation – many deserted estates show that it is very little better than the shifting cultivation of the hill man. It pays a coffee planter to take up a tract of primeval moist forest on our mountain slopes for a few years; he gets bumper crops the third, fourth and fifth years but denudation of the soil goes on rapidly and it does not pay him to keep it up many years. Can we restore the grand old forest with all its climatic influences? A thorny wilderness takes its place'. This was written 76 years ago. Vogt has presented the same grave picture as happening in the world today. Populations, he continues, have therefore to concentrate above 700 metres. The best agricultural land in the higher altitudes lies in the intermont valleys but in part, because there is an insufficiency of land and the best lands are in the hands of wealthy owners, the mass of farmers are crowded on the slopes where they practice shifting cultivation (*milpa*) which has resulted in a very high percentage of slopes throughout Latin America becoming de-vegetated. The usual results are of loss of soils and aridity, with flash floods with their consequent scouring action, interspersed with periods of little or no water in the rivers. Mr Vogt continues 'The land settlement pattern in Latin America has resulted in the extremely grave situation that there exists probably from *twenty to forty million displaced persons.* They are displaced in the ecological sense, namely that their present relationship to the land is destroying it at an accelerating rate, not only in the highland areas where they live, but in the lower areas affected by river flows. Many millions of acres of soil have become seriously eroded in Latin America and, as Professor Stebbing has described in the case of the Sahara, deserts are on the march. One of the worst instances of this land pathology is in St Salvador, where two million people, increasing at the rate of forty thousand a year, have available for agriculture only about an acre *per capita*, and much of this land is of low productivity'.

How many displaced persons, using the term in Vogt's sense, are there at the present moment in Africa? It is a natural query. We may also ask at what accelerated pace, compared with the past, are the processes of degradation in erosion, desiccation, sand penetration–the term varies with the conditions being produced – proceeding in Africa today? According to French investigators the Sahara has advanced southwards during the last three centuries at the rate of half a mile a year!

From the studies I have made I would record the opinion that a belt of country in Africa between the 13° and 15° parallels of latitude and stretching from French Senegal in the west at El Obeid and Kosti on the White Nile in the Sudan to the east, is at the present day in the Intermittent Rainfall stage, and is still in a condition when man may undertake operations to stop further degradation and the onward march of the desert. It is impossible, nor is it necessary, to deal here with practical methods which could be undertaken.

THE INFLUENCE OF CLIMATIC FACTORS ON THE REACTION OF DESERT SHRUBS TO GRAZING BY SHEEP

Professor H. C. Trumble, and K. Woodroffe*

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The arid pastoral areas of southern Australia with a mean annual rainfall of less than 10 inches are characterized by species of *Atriplex* and *Kochia* which occur extensively as low growing shrubs. These plants are well adapted to withstand rainless periods of long duration, and they provide reserves of feed in unfavourable seasons. The shrub cover has been greatly depleted by grazing sheep for approximately a century, and much land has been completely denuded. As viable seed of these shrubs no longer occurs in significant quantity, natural regeneration of perennials is rare on such country. Artificial seeding is costly and hazardous owing to low and uncertain rainfall. Sheep-raising in these areas is now largely dependent on annual herbage, and thus has become more subject to the risks of unfavourable seasons.

In other parts of the pastoral country, relatively undamaged associations of perennial shrubs still occur. Fairly extensive areas carry a moderate to sparse population of shrubs which produce seed in favourable seasons, making possible some natural regeneration. Investigations of pasture management here should throw light on the reaction of desert shrubs to grazing by sheep, and hence suggest more effective and permanent systems of utilization in arid regions. A previous investigation (Osborn, Wood and Paltridge, 1932) has indicated that pastures of saltbush (*Atriplex vesicaria*) may be improved under certain conditions of grazing.

Researches were commenced in 1941 at Yudnapinna Station, approximately 250 miles north-west of Adelaide; this centre is within the extensive North-west Pastoral District of South Australia. Investigations of the ecological factors concerned with the grazing management of bluebush (*Kochia sedifolia*) and associated species were undertaken on a long-term basis.

Climatic Factors

A meteorological station (Fig. 1) was established at Yudnapinna in October, 1938 and daily records of air temperature, relative humidity, wind mileage, free water evaporation and rainfall have since been maintained. Rainfall had been measured previously from 1885 onwards, thus giving an uninterrupted record to date of 67 years. The mean annual rainfall is 7.92 inches with a range from 2.36 inches to 18.08 inches per annum, and a modal frequency of between 5 and 6 inches.

Although the mean rainfall is fairly evenly distributed through the year, winter rains are more frequent and dependable; the mean monthly rainfalls for the period May – August are slightly greater than for the remainder of the year. In summer the precipitation tends to occur spasmodically as extremely fortuitous but heavy rains.

* The authors have been jointly responsible for the planning of the work described and the analysis of the data recorded; but the detailed investigations and most of the observations made are attributable to Mr K. Woodroffe, and will be the subject of a subsequent paper by him.

Figure 1.
The Meteorological Station, Yudnapinna.

Summer temperatures are high, and the daily mean temperature from November to March exceeds 70°F. The rate of evaporation from a free water surface is high during summer, with a maximum of 14.5 inches in January; evaporation falls to a minimum of 2.6 inches in June. (Table 1.)

Due to lower evaporation, winter rains are more effective for plant growth than summer rains of equal magnitude and use has been made of the index $P/E^{0.75}$ (Prescott, 1949) to define the minimum influential rainfall for each month. On the basis of observations on plant response and monthly records of soil moisture in the root zone, a monthly value of $P/E^{0.75} = 0.2$ has been found to indicate the lower limit above which soil moisture tends to become available, and new growth therefore possible. (Table 1.) Rainfall in excess of $0.2E^{0.75}$[1] constitutes water available for transpiration, to which the amount of herbage growth can be related.

The pattern of influential rainfall for the period 1885-1951 (Fig. 2.) indicates clearly the predominance of favourable growing conditions during the restricted period

[1] For the month of June, the value of 0.41 derived from the above expression has been increased to 0.5 to allow for the more frequent light falls of only a few points each in this month.

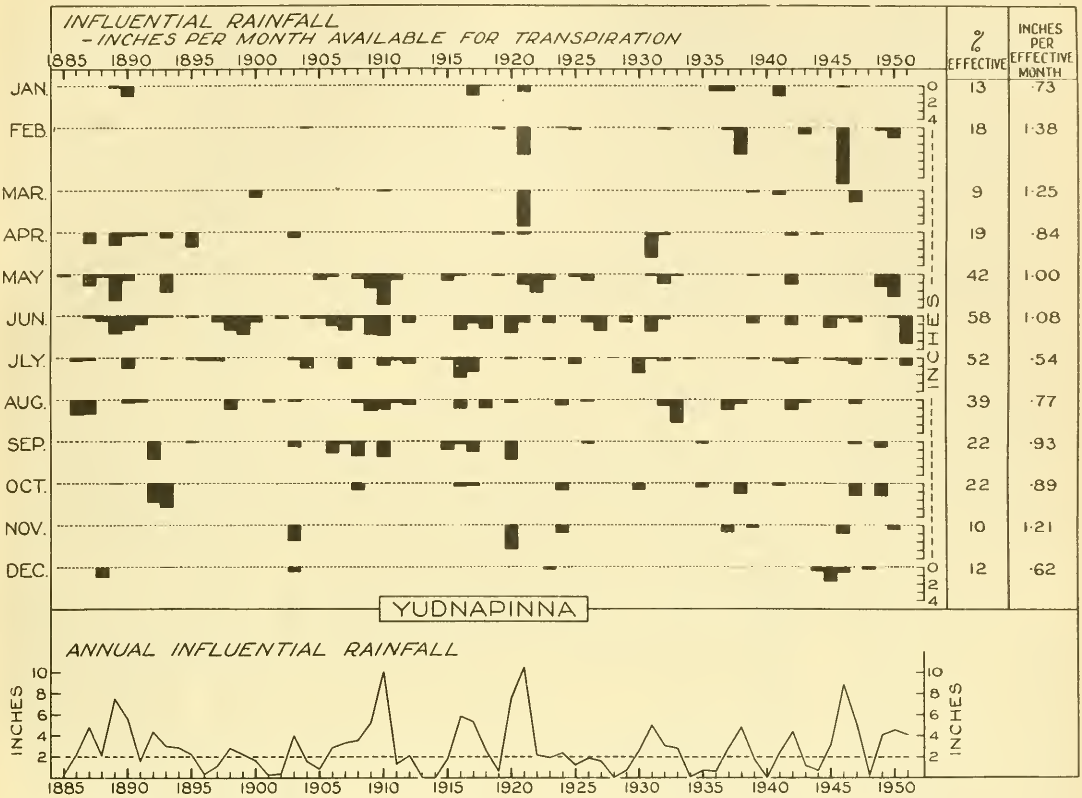

Figure 2.

Influential Rainfall — inches per month available for transpiration — Yudnapinna.

of May to August inclusive, and particularly in June. The expected occurrence of monthly rainfall exceeding 4S.D $^{0.75}$[1] (Table 1.) confirms the greater reliability of favourable soil moisture conditions in winter, (Cornish, 1952). The monthly values for influential rain have been summed to give a seasonal value; the mean influential seasonal rainfall for 67 years is 2.85 inches and the mean number of months with effective precipitation is 3.2 months per annum. Years with a seasonal value of less than 2.0 inches of effective rain have been classified as drought seasons, and those with a value greater than 2.0 inches have been classed as seasons favourable for herbage production.

The amount of growth that can be made on limited quantities of available moisture has been assessed in field and glasshouse studies of transpiration in relation to growth. These indicate an average value for *Kochia* and *Atriplex* spp. of 3 cwt. dry material per acre inch of water transpired, and this appears to be capable of supporting a sheep on 20 acres, or 32 sheep to the square mile for a period of 12 months.

[1] 4S.D $^{0.75}$ is equivalent to 0.4E $^{0.75}$ (Prescott, *et al.*, 1952).

TABLE 1

Climatic data, Judnapinna, (1939- 51)

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Mean length of day (hours)	13.9	13.2	12.2	11.1	10.3	9.8	10.1	10.8	11.8	12.8	13.7	14.1
Mean air temperature ^{o}F	78	76	72	63	58	52	51	54	59	64	70	75
Mean rainfall (inches)	.593	1.379	.588	.382	.818	.985	.694	.518	.412	.805	.721	.905
Mean evaporation from standard 36" evaporimeter (inches)	14.51	11.45	10.22	6.52	4.32	2.58	3.00	4.19	6.48	9.04	11.14	13.24
$.2E^{0.75}$ (inches)	1.5	1.2	1.1	0.8	0.6	0.4	0.5	0.6	0.8	1.0	1.2	1.4
Calculated probability of rain exceeding $4S.D.^{0.75}$	.028	.032	.019	.082	.269	.576	.408	.292	.183	.079	.032	.007

Mean annual rainfall (1939- 51) – 8.80 in.

Mean annual rainfall (1885- 51) – 7.92 in.

Examination of the seasonal pattern indicates a tendency for seasons of high or low rainfall to bunch together. The sequential nature of dry and wet winter seasons is apparent; the May – August rainfall, and particularly the June rainfall, exhibit a marked suggestion of periodicity. The annual rainfall of the Station, plotted as 10-year running means (Fig. 3.) and extrapolated back prior to 1885 by correlation with other records, and the notes of early explorations, appears to indicate a long-term repetitive pattern of 20-25 years of increased rainfall, (e.g. 1870 – 1895) followed by periods of 10-12 years of much lower rainfall (e.g. 1895 – 1905).

The importance of the climatic factors and particularly the rainfall sequence to the behaviour of desert shrubs, and their utilization for sheep grazing, will be indicated in the subsequent discussion.

Pasture Management.

Investigations of pasture management at Yudnapinna have been based essentially upon a long-term grazing experiment in which bluebush (*Kochia sedifolia*) pastures have been subjected to differential rates of stocking with sheep, on thirteen plots of 160 acres each since April 1941. The pasture (Fig. 4) consists of an open community of *Kochia sedifolia* with a mean density of 380 bushes per acre at the commen-

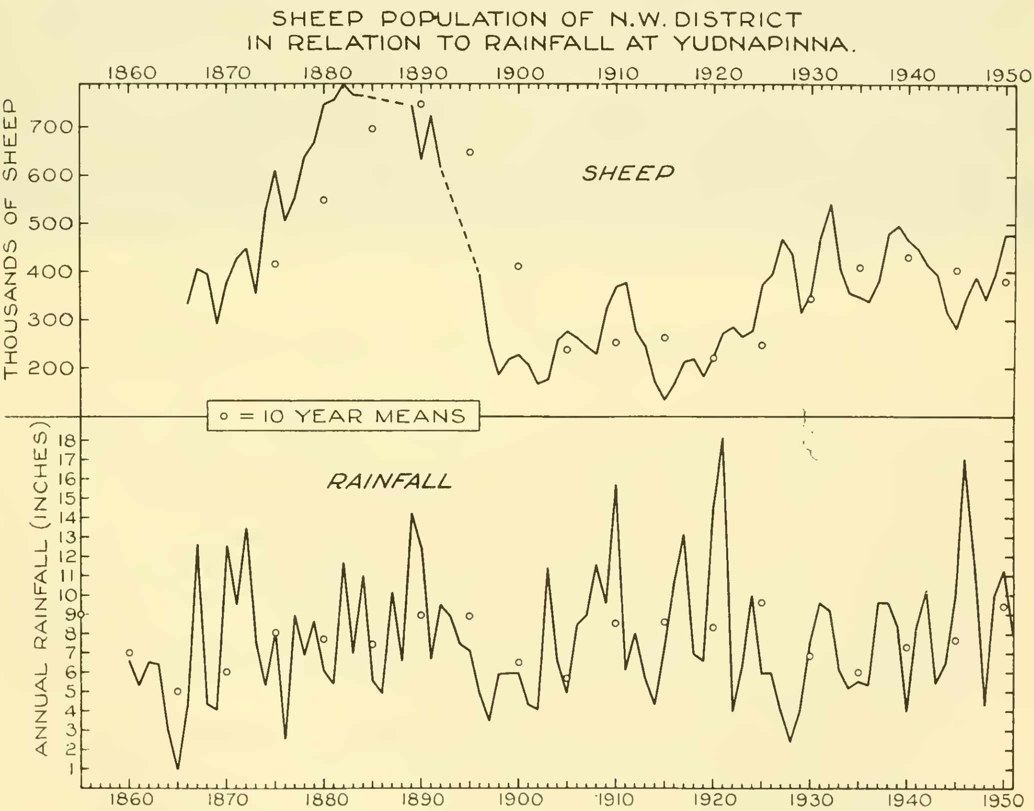

Figure 3.
Sheep population of N.W. District in relation to rainfall at Yudnapinna.

Figure 4.

Kochia sedifolia pasture, with myall trees (*Acacia sowdenii*); grass and other annuals complete with the bluebush which is not growing vigorously.

cement of the experiment. Myall trees (*Acacia sowdenii*) and a number of shrubs of minor importance are associated with the bluebush. During drought years the ground between the bushes is devoid of plants, but in seasons of favourable rainfall, herbage and grass provide a sparse to moderate cover. The soil is of an arid calcareous type, with a brown loamy sand surface; the texture increases gradually to a sandy clay at about 3 feet. The effects of treatments have been measured primarily by weight estimates (Woodroffe, 1941) of the amount of edible green forage present in the spring of each year; trends in the numbers and production of bluebush have been used as the main indicators of the results of grazing. Live weights and wool production of the sheep have been recorded.

For the purpose of the present paper, discussion will be confined to five treatments, viz:-

1. Control with no grazing.
2. Continuous light grazing at the rate of 24 sheep per square mile.
3. Continuous moderate grazing at the rate of 48 sheep per square mile.

4. Continuous heavy grazing at the rate of 72 sheep per square mile.
5. Intermittent very heavy grazing at a mean rate of 128 sheep per square mile; average 90 per square mile 1941 - 1946 and 168 per square mile 1947 - 1951.

The amounts of bluebush forage and the numbers of bluebush per acre over the period, 1940 (before commencement of grazing) to 1951 are shown in Tables 2 and 3. The weight of bluebush on all treatments fluctuated from season to season and was related to the influential seasonal rainfall (Fig. 5); the green weight of edible blue-

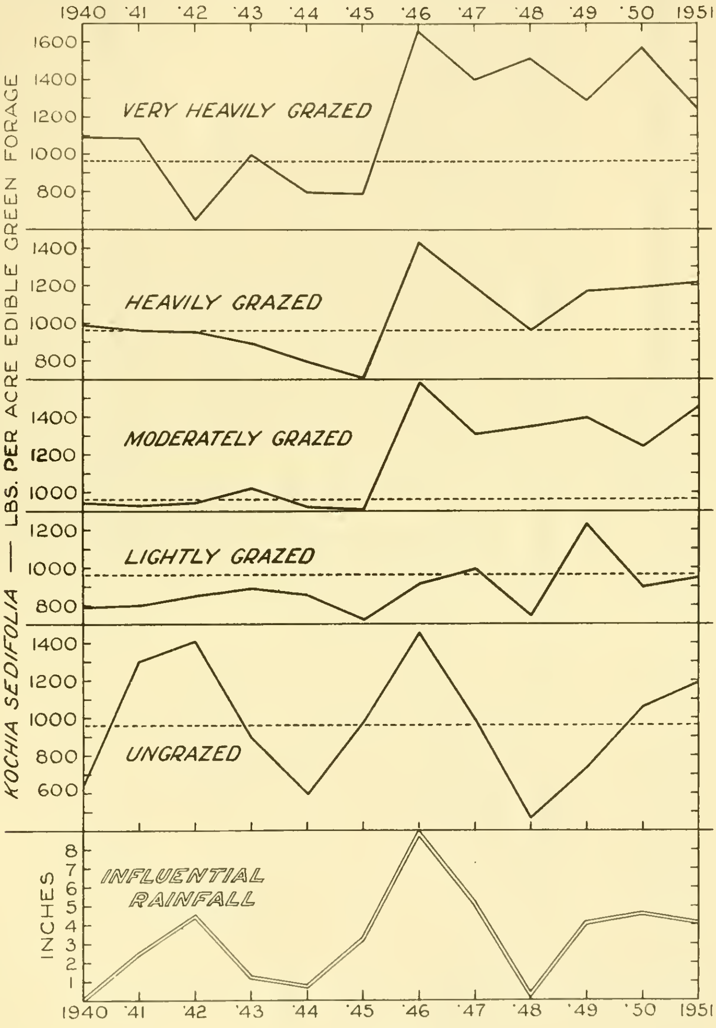

Figure 5.

Weight of *Kochia sedifolia*, estimated in September, on plots grazed at different rates of Stocking — Yudnapinna.

Actual weights of forage are shown for the ungrazed control plot to indicate seasonal fluctuations. For the grazed plots weights of forage have been adjusted relative to the ungrazed plot to eliminate the direct effects of season, and the mean of the ungrazed plot (broken lines) is shown for comparison.

TABLE 2

Bluebush forage (lb./acre green material) on different grazing treatments, Yudnapinna

Rate of Stocking		1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951
Nil		650	1300	1410	900	580	970	1450	980	470	730	1060	1190
Light	(24/sq. mile)	500	1080	1240	820	510	720	1330	990	300	960	970	1140
Moderate	(48/sq. mile)	590	1290	1430	940	490	910	2110	1320	730	1050	1340	1700
Heavy	(72/sq. mile)	690	1260	1360	830	420	700	1870	1200	500	870	1260	1420
Very heavy	(128/sq. mile)	640	1540	1270	900	260	790	2340	1410	810	850	1700	1550

TABLE 3

Numbers of bluebush per acre on different grazing treatments, Yudnapinna

Rate of Stocking	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951
Nil	510	560	580	620	590	730	750	730	680	630	630	630
Light (24/sq. mile)	290	360	400	480	480	500	550	580	490	450	450	450
Moderate (48/sq. mile)	500	570	570	610	600	660	870	1040	700	680	680	670
Heavy (72/sq. mile)	440	490	490	530	540	590	1050	1120	880	730	730	700
Very heavy (128/sq. mile)	420	490	500	550	500	550	1490	1750	1620	1390	1200	1220

bush in September on the control plot ranged from 1450 lb. per acre in 1946 to 470 lb. per acre in 1948, with a mean of 970 lb. per acre over 12 seasons. The seasonal fluctuation in the amount of all other forage was much greater; its green weight on the ungrazed plot ranged from 2300 lb. per acre in 1946 to 15 lb. per acre in 1948.

It has been found possible by correlation and regression to eliminate the direct effect of season on the weight of bluebush forage in the grazed plots, and to convert these weights to a 'constant season' basis, represented by the mean of the control plot. (Fig. 5)

After accounting for seasonal variation, the amount of bluebush on the lightly and moderately grazed plots remained practically constant over the period 1940-1945, whereas there was a downward trend in the weight of bluebush on the heavily and very heavily grazed plots. This trend was associated with heavy grazing of bluebush during three seasons of low influential rainfall, including two drought years, 1943, 1944, followed by only moderate rainfall prior to September, 1945. All plots responded to the favourable rains of 1946, but after eliminating the response due to season alone, there remained an extraordinary increase in the weight of bluebush on the moderately to very heavily grazed plots, which can only be ascribed to the more intensive grazing with sheep at the higher livestock concentrations. There was a small but less marked residual response on the lightly grazed plots. Since 1946, the seasons have been unusually favourable, with the exception of 1948, and on the three plots subjected to moderate to very heavy stocking the weights of bluebush forage, after some recession from the peak of 1946, have fluctuated about levels considerably in excess of their initial values. The high level has been maintained on the most heavily grazed plot despite an increase in the mean stocking rate from 90 to 168 sheep per square mile. The amount of bluebush on the lightly grazed plot has shown a gradual upward trend over this period.

Part of the increase in production of forage by bluebush on the grazed plots, relative to the ungrazed plot, is undoubtedly due to the substantial increase in the numbers of bushes on the former plots from 1944 to 1946. (Table 3.) A heavy seeding of bluebush occurred early in 1945, and large numbers of seedlings germinated on all plots, including the control. The greater vigour of the seedlings on the grazed plots, and particularly where grazing was heaviest, was most noticeable and accounted for the larger number of young plants which became established on these plots. (Fig. 6) Within the grazed plots, a greater increase in numbers of young plants occurred towards the southern end of the plots. (Table 4.) Sheep graze into the prevailing southerly wind, with the result that this part of a paddock is inevitably most heavily grazed.

The increase in the weight of bluebush per unit area was not entirely due to increase of numbers, and indeed, on all the stocked plots except those most heavily grazed, the numbers have since fallen to levels comparable with the ungrazed plot. The increased vigour and leafiness of the older bluebush on the heavily grazed plots, compared with the ungrazed control, have been outstanding. Moreover, the larger numbers of stock on the heavily grazed plots have been successfully carried in prime condition, and with only a slight reduction in wool production per head.

This result can only have become possible through higher protein production per unit of soil water available for plant growth. Increasing nitrogen concentration and protein formation per unit of water transpired would have been favoured by heavier defoliation (Trumble, 1952), and the greater concentrations of livestock might also have tended to enhance nitrogen enrichment of the soil *per se*.

TABLE 4

Increase in numbers of bluebush per acre from 1944 to 1946 over southern and northern halves of plots

	Rate of Stocking				
	Nil	Light	Moderate	Heavy	Very heavy
Southern half	190	110	400	690	1500
Northern half	130	30	140	340	480

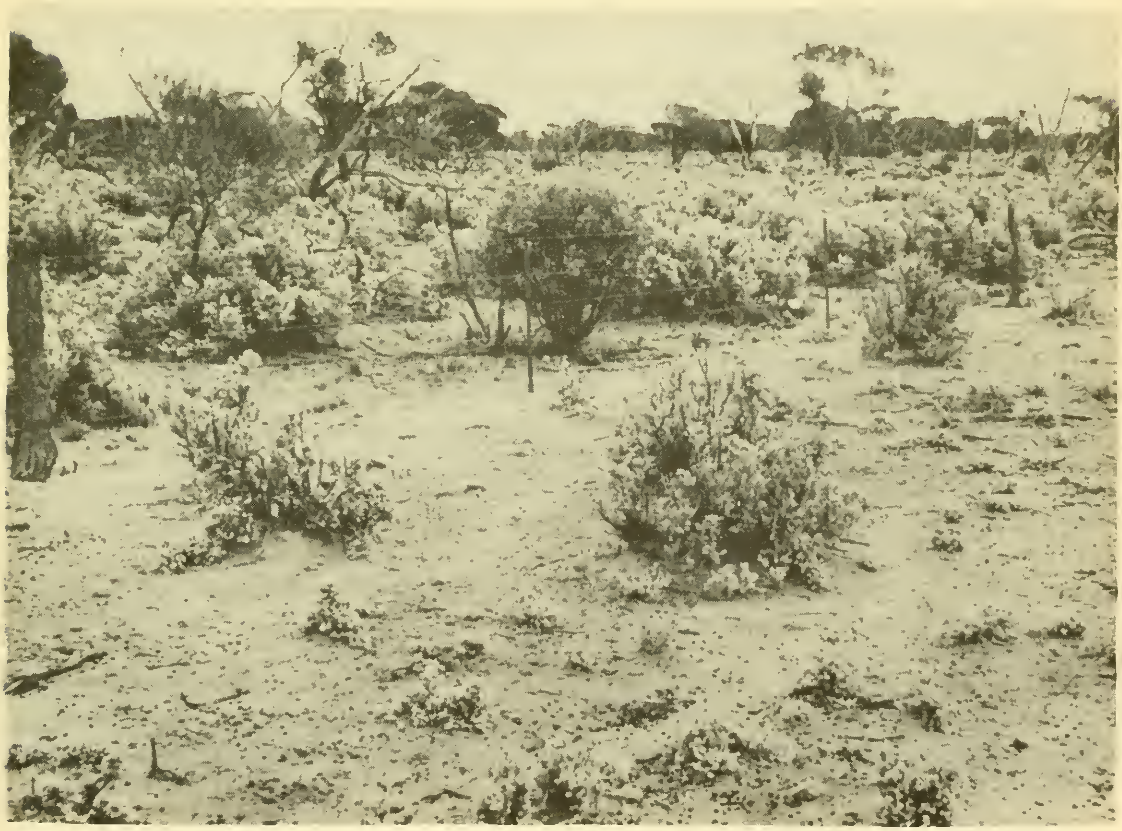

Figure 6.
Heavily grazed bluebush in foreground showing active regeneration of bluebush; moderately grazed plot with less regeneration in background.

The improvement of shrub pastures of *Kochia* and *Atriplex* under moderate to heavy but not too severe stocking has been frequently noted by pastoralists, and was recorded in the investigation of the effect of grazing on *Atriplex vesicaria* (Osborn, Wood and Paltridge, 1932). The greater vigour of grazed stands has been attributed to pruning of the bushes leading to the production of young shoots. This probably results in the conservation and more efficient subsequent use of soil water reserves, but does not in itself account for the increased establishment of young plants. The Chenopodeaceous shrubs are less palatable to sheep than much of the annual herbage, and it is possible that part of the increase in number and production of shrubs may be due to the control of competing annuals by grazing. In the present experiment, however, the weight of forage other than bluebush on all the grazed plots except the very heavily stocked plot, has at least equalled that on the control plot over the period 1946-1951.

Previous investigations with the perennial grass *Phalaris tuberosa* (Richardson, Trumble and Shapter, 1932) showed that repeated defoliation trebled the amount of nitrogen in the edible above-ground portion of the plant compared with that contained in previously ungrazed herbage. Approximately one half of this increase was secured by the herbage at the expense of the nitrogen in the root system and other portions of the plant not available to livestock. The remainder of the increase was assumed to be the result of increased uptake of nitrogen from the soil.

A major factor responsible for the marked improvement of the bluebush on the grazed plots relative to the ungrazed is considered to be the increase of soil fertility through the grazing animal, a principle that is widely accepted on pastures in areas of higher rainfall, particularly where phosphatic fertilizers are applied (Trumble and Donald, 1938; Sears and Goodall, 1948), but which so far as the authors are aware has not been recognized in arid regions.

The Fertility Status of Arid Soils

Although climatic factors are of paramount importance in determining the productivity of semi-arid and arid regions, it is now evident that the limiting role of soil fertility must also be considered. The level of fertility is in part a reflection of prevailing climatic conditions which limit the physical and chemical processes of soil formation as well as biological and microbiological activities. The breakdown of rock minerals proceeds slowly, profile characteristics are generally not well developed, and soluble salts may accumulate; soil organic matter and soil nitrogen are invariably at a low level. In some cases the geological parent materials of the soils are low in essential nutrients and the soils developed from them are correspondingly deficient.

In the arid pastoral areas of southern Australia the principal soil groups are arid red earths, stony tableland soils and arid calcareous soils. *Atriplex vesicaria* and *Kochia planifolia* are the more important shrubs associated with the two former groups, while *Kochia sedifolia* is associated with the arid calcareous soils. The soils of the North-west Pastoral District have been developed on Cretaceous shales, and Jurassic sandstones of low nutrient status (Jessup, 1951), whereas in the North-east Pastoral District the soils are associated with richer Proterozoic and crystalline

Archaean rocks. Pedogenetic considerations, therefore, indicate a lower fertility level for the north-west soils and this has been confirmed by practical observation of herbage responses following rains and the stock fattening capacity of the two districts.

As part of the present study, the productivities of a range of semi-arid and arid soils were compared in a series of pot culture tests with that of a moderately fertile red-brown earth soil from the Waite institute and representative of the better agricultural areas of the State. (Table 5- Fig..7)

The results indicate the low fertility of the arid soils and particularly of those from the North-west District. Marked responses were obtained to soluble nitrogen on all the arid soils although there was little response to phosphorus; even with the heavy application of nitrogen and phosphorus, however, the productivities of these soils were considerably below that of the red-brown earth, indicating the possibility of a further limiting factor or factors in the former soils.

One indication of the limitation of productivity imposed by deficient nutrient supply is given by the wide differences in the transpiration ratio for *Atriplex vesicaria* in pot culture tests (series A) conducted on the respective soils: on red-brown earth soil a transpiration ratio of 370 indicated a production of 5.4 cwt. dry forage per

Figure 7.
Growth of barley without fertilizer on various soils (left to right). Red-brown earth, Waite Institute; solonized brown soil, Pallamana; arid red earth, N.E. District; arid red earth, N.W. District.

TABLE 5

The productivity of various soils in pot culture
(Mean yields oven-dry herbage : gm. per pot)

Soil No.	Soil Type	Locality	Series A. Three species – No fertilizer			
			Barley	Rye	*Atriplex vesicaria*	
1.	Red brown earth	Waite Institute	110.0	95.3	87.0	
2.	Solonized brown soil	Pallamana	16.7	14.6	26.5	
3.	Arid red earth	N-E. District	17.3	13.7	20.7	
4.	Arid red earth	N-W. District	7.8	7.0	10.2	
			Series B. Barley with phosphorus and nitrogen			
			Nil	P_2	N_2	P_2N_2
1.	Red brown earth	Waite Institute	15.85	22.10	18.00	25.25
2.	Solonized brown soil	Pallamana	1.80	2.20	5.65	6.20
5.	Arid calcareous soil	N-E. District	6.35	6.25	9.35	9.80
6.	Arid calcareous soil	N-W. District	0.35	0.40	3.30	3.50
			Series C. *Atriplex nummularia* with phosphorus and nitrogen			
			Nil	P_4	N_4	P_4N_4
2.	Solonized brown soil	Pallamana.	4.93	6.48	10.97	12.09
6.	Arid calcareous soil	N-W. District	1.93	2.35	3.53	7.66
7.	Arid red earth	N-E. District	8.45	9.67	13.95	12.40
8.	Arid calcareous soil	N-E. District	4.58	4.52	10.34	10.54

Series A. – 4 replicates large pots.

Series B. & C. – 2 replicates small pots. P_2 and P_4 = 2 cwt. and 4 cwt. superphosphate per acre.
N_2 and N_4 = 2 cwt. and 4 cwt. sulphate of ammonia per acre.

acre inch of water transpired; by comparison, with material grown on north-west arid red earth, a transpiration ratio of 570 indicated a production of only 3.5 cwt. dry forage per acre inch of water transpired.

The fertility cycle under arid shrub vegetation

Comparatively little is known of the fertility cycle in arid soils, and any discussion is necessarily of a speculative nature. The soils of the North-west Pastoral District have low organic carbon and nitrogen contents of the order of .25 and .025 per cent respectively (Crocker and Skews, 1941; Jessup, 1952). The processes of breakdown and decay of plant remains are extremely slow, and despite a carbon nitrogen ratio of 10 : 1, it appears that the mineralization of the soil organic matter and particularly the production of nitrate is inhibited, partly by climatic conditions, but perhaps also by unfavourable soil conditions including possibly the presence of the root systems of perennial plants (Theron, 1951).

It appears legitimate, therefore, to regard the fertility cycle under natural conditions as an almost closed system with the nutrients circulating at an extremely slow rate, with a large proportion of the 'available' supply locked up at any given time in living or dead plant material and partly decomposed remains. There is, nevertheless, a small annual turnover of nutrients permitting limited production when soil moisture conditions allow plant growth. Nutrients may accumulate in the soil during a cycle of dry years when virtually fallow conditions prevail; then with the occurrence of favourable rains a relatively lush growth occurs which gives a misleading impression of fertility. But should another favourable season follow the first the soils are incapable of sustaining production and very little growth is made. This occurred at the Yudnapinna Station in 1947 following the previous good season in 1946.

The impact of the grazing animal on the fertility cycle of arid shrub pastures

The introduction of grazing animals to shrub pastures leads to a marked acceleration in the fertility cycle by increasing both the amount of plant material returned to the soil and its rate of decomposition. The rate of turnover of nitrogen in particular is accelerated because some 75 per cent of the amount ingested by merino sheep is returned to the soil in urine, and rapidly becomes available to plants. A further 20 per cent, returned in the dung, undergoes more rapid decomposition than non-ingested plant material. Provided conditions of rainfall are favourable, plant growth is stimulated by the fertilizing effect of the grazing animal; and the cycle is repeated at a rate depending on the stock concentration per unit area, on favourable temperatures, and on availability of soil moisture.

It is estimated that the large-framed merino wethers employed in the grazing management investigations under review (150 lb. live weight) void annually 25-30 pounds of nitrogen. On the most heavily grazed plot during 1946-51 the amount of nitrogen returned to the soil by the animal was of the order of 6-7 lb. per acre per annum. This represents a considerable increase of the soil nitrogen available, in terms of the relatively low production level on a per acre basis. On the more heavily grazed portions of the plot, the amount of nitrogen returned would have been corres-

pondingly greater. It is also possible that by the stimulation of greater microbiological activity in the manured soil, the rate of decomposition of the soil organic matter was hastened, leading to the release of further nutrient supplies.

The grazing animal can add little to the total store of fertility in arid soils in the absence of important leguminous constituents of the pastures, but by increasing circulation of nutrients, it may add greatly to the productivity of shrub pastures during favourable seasons. This may also stimulate the regeneration of young shrubs from seed. The drain on soil fertility by the removal of nutrients in animal products does not represent a serious loss when spread over many acres, and insofar as nitrogen is concerned, would not amount to more than ½ lb. per acre per annum in the above example.

The improvement of soil fertility by the fertilizing effect of sheep accounts satisfactorily for the observed effects on the shrub pastures in the grazing management investigation. During seasons of low rainfall the pasture did not benefit from the return of nutrients; and the weight of forage per acre was depleted on the heavily and very heavily grazed plots. During this period nutrients accumulated in the soil in a fairly readily available form in the plots grazed at moderate to very heavy rates of stocking. Under the favourable climatic conditions of 1946, the established shrubs responded to the accumulated sheep manure. Young seedlings developed vigorously and were able to become firmly established, leading to a large increase in bush density. Under the subsequent generally favourable conditions of 1947-51, the circulation of nutrients was maintained and the production of herbage continued at much higher levels than on the ungrazed plot.

Hence the productivity of shrub pastures may be regarded as a function of grazing intensity and effective seasonal rainfall; and high intensities of stocking can only be maintained during favourable seasons, since the fertility cycle pasture – animal – soil – pasture can only operate when there is sufficient soil moisture available for sustained plant growth. It is probable that repeated heavy defoliation of shrubs during a run of drought seasons would lead to widespread mortality of the bushes. This concept of grazing intensively the arid shrub pastures when seasonal conditions favour their active growth makes possible substantial improvement in practical management.

There is of course a limit to the number of sheep which may be carried on shrub pastures during seasons of high effective rainfall. An equilibrium must be maintained between growth and consumption of forage. The small size of the grazing areas employed in these investigations has permitted the support of sheep at rates greatly in excess of the recognised carrying capacity of shrub pastures in the North-west District where the average stocking rate is 25 sheep per square mile (Jessup, 1951). The mean size of paddocks in this area is, however, 32 square miles with an average of only one watering point per paddock (Jessup, *loc. cit.*). Under these circumstances, the upper limit of carrying capacity beyond which permanent degeneration of the shrub stand may occur is fixed by the stock concentration within a ½ mile radius of the water supply.

Sheep population in relation to the seasonal pattern

Efficient utilization of shrub pastures through intensive grazing during periods of active growth can only be attained by fitting stock numbers to the long term rainfall pattern, which is the primary determinant of forage resources; and by close subdivision of pastures together with the provision of adequate watering places. In this way, maximum production will be attained, stock losses avoided, and the pastures either improved or maintained in a sound condition. If, on the other hand, the numbers of grazing animals are not so adjusted, pastures either may not be utilized effectively, or may be permanently damaged in attempting to maintain high numbers during a sequence of drought seasons.

The Yudnapinna rainfall records reflect the seasonal pattern for the North-west District, and the record of sheep population in this area (Fig. 3) shows that stock numbers have not been well adjusted to the broader rainfall trends.

The years 1870-1951 may be grouped into five main periods characterized by particular trends in rainfall, pasture status and livestock population.

First period (1870-1895). The sheep population of South Australia increased from the middle years of the nineteenth century to a maximum in 1890 (Davidson, 1938) largely by expansion to virgin pastures, including those of the North-west District. In this area numbers rose during a succession of generally favourable seasons from 374,000 in 1870 to 789,000 in 1882, a sheep density which the pastures could not permanently support under the existing conditions of subdivision and water supply. In the second phase of this period, from 1882-1895, the number of sheep maintained decreased to 618,000 by 1892, and to a still lower figure in 1895 for which no record is available. It is certain that considerable deterioration of the pastures commenced during these years.

Second period (1895-1905). The years of high rainfall prior to 1895 were followed by a succession of dry seasons from 1895-1905. Pastures had been gravely overstocked; sheep were concentrated on the few permanent waters, and the adjustment to drought conditions was enforced by sheep losses rather than by planned destocking; numbers fell to 275,000 in 1905. Extensive damage to the perennial shrubs occurred during this time, and their productivity in many cases was permanently impaired.

Third period (1905-1924). The third period from 1905-1924 was on the whole characterized by above average rainfall, but despite this, stock numbers tended to remain at a depressed level of about 250,000 sheep; it seems probable that the previous degeneration of the shrub pastures was a major factor. This period may be divided into three phases. The first phase from 1905-1911 was characterized by favourable rainfall; over this period the sheep population rose from 275,000 to 376,000, due to temporary recovery of the forage resources. In the second phase from 1911 to 1915 the degraded pastures were unable to provide forage during a recession of rainfall, and stock numbers decreased to 132,000 in 1915. Only a limited increase to 278,000 sheep occurred in the third phase of exceptionally high rainfall from 1915-1924, during which wartime labour shortage exerted some control. It

is likely that a considerable regeneration of shrubs occurred in this portion of the third period.

Fourth period (1924 - 1936). The sheep population increased from 278,000 to 314,000 during a sequence of dry years from 1925 - 1929 inclusive, as a result of regeneration of pastures during the previous stage. Numbers continued to increase to 540,000 sheep during the short term phase of high rainfall 1930 - 1932, but receded to 338,000 with the resumption of the dry cycle to 1936. The general level of sheep numbers rose from a ten year mean of 220,000 at the beginning of the whole period to one of 400,000 at the end.

Fifth period (1936 - 1951). The mean level of 400,000 sheep reached in the previous stage has been maintained, with some fluctuations, during the recent period from 1936 - 1951, indicating that at this level sheep numbers are in equilibrium with the present condition of the pastures. The general pattern of high rainfall over these years is interspersed with two short phases of unfavourable seasons during which the recession in sheep population was aggravated by wartime conditions. From 1945 - 1951, numbers of sheep rose from 318,000 to 478,000; during these favourable seasons very marked regeneration of shrubs has occurred.

The pastures of the region are now at a stage when sound measures of management related to foreseeable rainfall trends can lead to a considerable degree of improvement of both the capital resources and permanent productivity. On the other hand, a repetition of earlier mismanagement may lead to another recession of the pastures and widespread denudation. The investigations at Yudnapinna have indicated that greatly increased productivity may be achieved by a closer subdivision of pastures and the provision of better and more frequent water supplies.

Conclusions

The more effective utilization of arid and semi - arid pastoral areas depends upon the recognition of four outstanding principles :-

(1) An analysis of the climatic resources, and especially rainfall, in the long-term, with due allowance for evaporation rates and the inevitable groups of drought years.

(2) The use of fencing to provide for appropriate grazing management.

(3) Multiplication of the points at which livestock can secure water.

(4) The adjustment of stocking rates to the variations of the forage supply which are consequent upon the long - term climatic pattern.

These principles are of general application to arid regions and their adoption could lead to a very substantial increase in the productivity of both hot and cold deserts, provided (a) that there is a minimum quantity of moisture available for transpiration of the order of 2 inches per year and (b) that growth is not inhibited by low temperatures, of the order of monthly means of 40 - 45°F or less, during the period over which moisture is available to plants of value for permanent grazing.

Summary

Perennial shrub species of *Atriplex* and *Kochia* originally dominated the arid pastoral areas of southern Australia with a mean annual rainfall of less than 10 inches.

These pastures have been stocked with sheep for approximately a century; over-grazing, leading to denudation, has been marked. Some undamaged associations of shrubs remain, and some regeneration has occurred, but for the most part recovery of the pastures has been limited.

On both relatively undamaged and degraded country there is scope for improved methods of utilization. A study of grazing management within the North-west Pastoral District of South Australia conducted over a period of 11 years is described.

The climatic factors, and in particular, the rainfall characteristics of the area, have been analysed in the short and the longer term; and these have been related to the reaction to grazing of *Kochia sedifolia* and to major trends in the sheep population.

Marked improvement in the density and vigour of *Kochia sedifolia* resulted from intensive stocking during favourable seasons. The reaction of this shrub to grazing is explained in terms of an increased circulation of nutrients from the vegetation to the soil *via* the grazing animal, and thence back to the plant. A reduction of competing herbage, and more effective use of soil moisture by the shrub, as a consequence of its pruning by sheep, are contributing factors.

The general application of the principles discussed in the paper may lead to more effective utilization of the pastures associated with arid and semi-arid regions.

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BIOLOGICAL RESEARCH AND THE PRODUCTIVE TRANSFORMATION OF STEPPE AND DESERT IN THE SOVIET UNION

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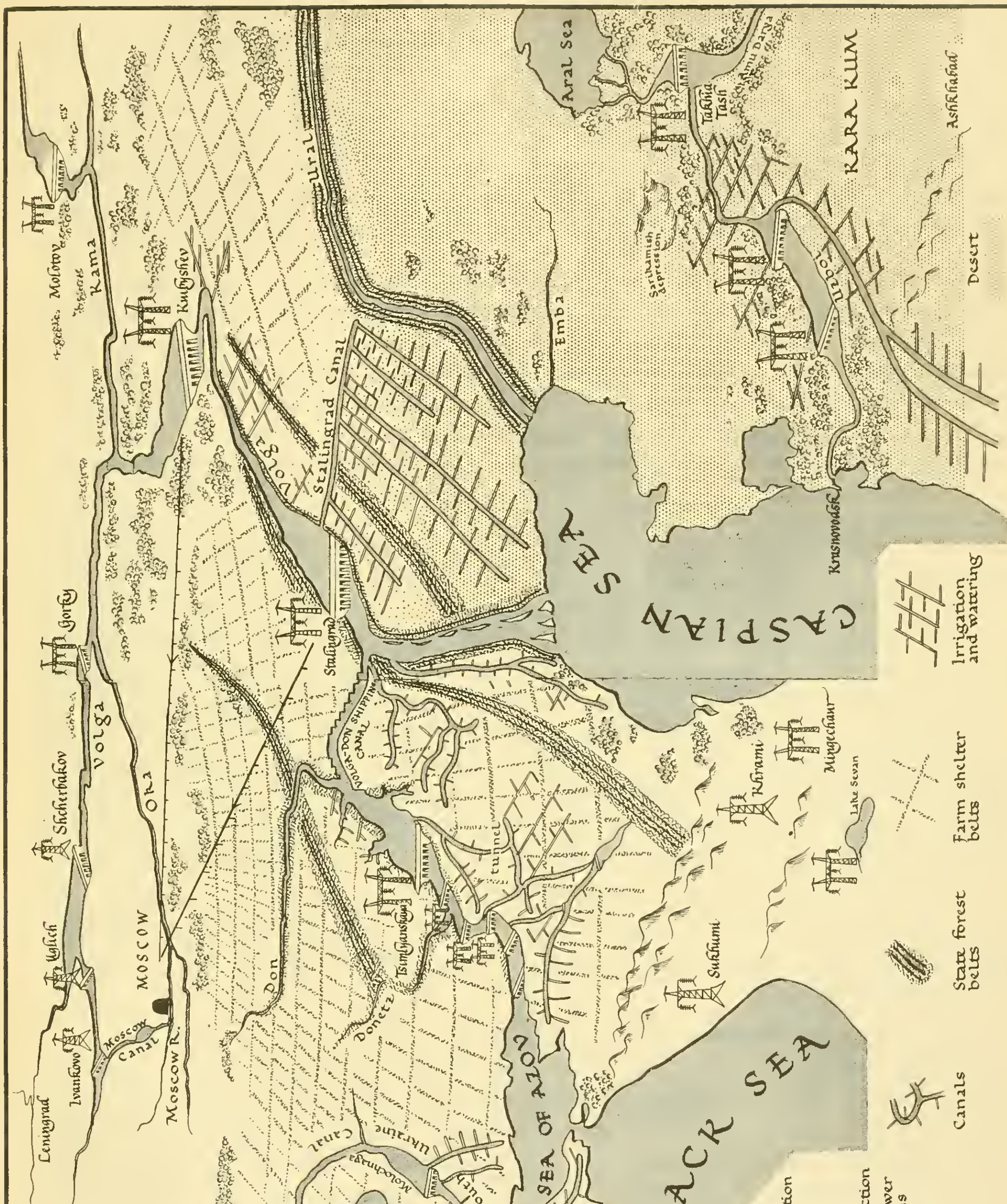
This communication does not concern any aspect of my own research but refers to the many lines of work which are in progress connected with increasing the productivity of the central Asian desert regions. In the summer of 1951 I accepted an invitation to visit the Soviet Union to meet scientific colleagues and to see something of their work. I travelled as far as central Asia, where I saw much of the speedy development of the country, of the modern laboratories in the Asian states and of the work connected with irrigation and afforestation, and the control of factors which limit animal and plant life over vast areas.

One million square miles of the Soviet Union is steppe and desert, and three quarters of a million of these form the central Asian deserts. Rainfall of between 2 and 15 inches occurs in spring and autumn, but not in the summer, and dry desiccating winds, at times of hurricane force, sweep from the Asian deserts westwards across the south Ukraine.

A fifteen year afforestation scheme was started in 1948, a quarter of which had already been completed. For hours I flew across the featureless steppe, now marked by black stripes. Each of these consisted of ploughed land 25-65 yards wide, and carried lines of seeded or seedling trees separated by low growing crops such as rye or clover which prevent weeds from smothering the young trees. Three thousand three hundred miles of major tree lines are being planted. Watershed lines, each up to 370 miles long, will interrupt the stream-lined air flow of the lower atmosphere, substituting turbulence, which will reduce the desiccating power of the winds. Tree lines are flanking river valleys for distances up to 700 miles, windbreaks are appearing between farms, and around natural erosion scars, which will not only check further erosion, but add humidity to the air and soil.

Twenty years of research has gone into establishing successful methods of cultivating trees under steppe conditions, as I saw on the research stations and in the field. Oak is being used to initiate the steppe forests because it develops a deep root system in dry soil. An abundance of tree planting machinery is being employed, but when acorns and not seedlings are planted, the appropriate mycorrhiza is added to the soil along with the acorns. Laboratories are occupied with the grading of acorns and other forestry work.

In 1950 hydro-electric developments were started which by 1957 will irrigate an area of 70 million acres, 20 million of these lying in the Asian deserts, and thereafter the acreage will increase still further. The newly made dam on the Don, with its half a mile central spillway of steel and concrete and 8 miles of earth wings, is sending water to the first quarter of a million acres of newly irrigated land this summer. Elsewhere in European Russia dams are being built to retain most or all of the spring flood water of the Dnieper and Volga. Six hundred miles of canals will carry water to


Leningrad
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Moscow R.
Don
Donetz
Stalingrad
Stalingrad Canal
Volga
Ural
Emba
Aral Sea
Takhia Tash
Amu Darya
KARA KUM
Ashkhabad
Desert
Sarikamish depression
Uzboi
Krasnovodsk
CASPIAN SEA
Mingechaur
Khrami
Lake Sevan
Sukhumi
Tsimlyanskaya
VOLGA-DON SHIPPING CANAL
tunnel
SEA OF AZOV
BLACK SEA
CRIMEA
Kakhovka
Dnieper
Molochnaya
South
Ukraine Canal
in operation
under construction
Hydroelectric power stations
Afforestation of sandy areas
Canals
State forest belts
Farm shelter belts
Irrigation and watering

the South Ukraine and north Crimea, and the Volga is being converted into a series of lakes up to 370 miles long. A canal of 375 miles is being made to carry a flow equal to that of the Don for the irrigation of an area of semi-desert equal to England in area, between the Volga and the Ural rivers. Besides canals, 44,000 water basins are being created, and hydro-electric power from new stations (with an aggregate capacity of four and a quarter million kilowatts) will pump water on to the land and drive agricultural machinery such as tractors, etc. The European schemes affecting the steppe will be completed by 1956, and the desert irrigation is to be effective by 1957.

The deserts of central Asia are partly man made, but the whole region has been drying up for thousands of years, although the cutting down of trees has worsened conditions. In the 3rd-4th millenium BC there were towns 12 miles across in the present desert areas, and archaeological evidence shows the existence of past irrigation systems. At one time a branch of the Amu Darya river flowed across Turkmenia to the Caspian sea. The fertility of much of the desert is seen in the small scale irrigated areas of Turkmenia, and in the large oases, such as Tashkent, which supports a population of 1,300,000.

Work has now begun on the building of a dam across the Amu Darya near its delta to the Aral sea for the purpose of deflecting about 47% of its flow into a 683 mile canal across Turkmenia to Krasnovodsk on the Caspian Sea. Another 746 miles of branch canals will irrigate about three and a half million acres (5,000 square miles) of desert. The middle section of the canal which will use the dried up bed of the Uzboi river, now many feet thick in salt, will flood about 17 million acres (27,000 square miles) for periods of from one to three months, so providing increased pasture for horses, cattle and karakul sheep. The average daily flow on the canal will be about 6,500 million gallons (4 times that of the Thames), but at times will be double this figure. All the water at present will be used for irrigation, and none will pass on to the Caspian Sea. A project of this magnitude has not been attempted anywhere in the world.

The associated scientific work serves two purposes. Firstly there is the preliminary work connected with the actual construction and maintenance of such a desert canal, and secondly much work is in progress concerning the maximum productivity of the land to be irrigated.

The preliminary work has been in progress on a considerable scale. By 1951 a scientific base was in working order in the Kara Kalpak, with a newly built railway line, and a feed canal to supply water for the workers, for hydraulic machinery and for the local growing of crops. Three hundred scientists were at work there in the summer of 1951 and their number had increased to 500 by the spring of 1952. In addition there are many field parties, and a large scale photo survey has already been made from the air.

The subsoil waters in the Kara-Kum desert are of greater importance than the surface waters, and they are being investigated by parties of geologists, each numbering about a dozen, and equipped with drilling apparatus. Underground fresh water streams can in places be deflected to the surface, and in fact now water the town of Krasnovodsk. The salinity and rates of seepage of subsoil waters is being determined, as saline water

must on no account be raised to levels which would effect crops by seepage of water from new canals. Seismological parties are studying the structure of geological strata by measuring tremors caused by explosions.

Meteorological stations have been set up in many places in the Caspian lowlands and Asian deserts to collect data which, among other things, may give information concerning the origin of the dry desert winds referred to above, and assist in combating sandstorms. A special laboratory for the study of sandstorms has been set up in the Ashkhabad by the Turkmenian branch of the Academy of Sciences of the U.S.S.R.

Protection of both canals and of irrigated land in the desert against shifting sand and wind are essential. Shelter belts of poplar trees can be quickly grown when watered; they now form wind breaks round the fields of Tashkent and other oases, but unlike the steppe forests, these poplar windbreaks depend on irrigation. Altogether one and a quarter million acres of desert forest will be grown to shelter the canal and the watered land; this work is co-ordinated by a special Ministry of Forestry for the construction schemes. The Black Saxaul tree grows without irrigation in the desert, and was once more widespread in occurrence than at present, having been cut down for fire wood. In the summer of 1951 seeds of this tree were collected, and in the spring of 1952 were sown over large areas by parties operating from camels (this traditional ship of the desert is now very little used). The black saxaul sends its roots down to a depth of 30 feet, thus fixing the soil as well as gaining moisture, and in 10 years it can reach a height of 20 feet and a trunk girth of 1 foot. The controlled use of this tree should provide substantial yields of timber within 25 to 30 years. Ash, white acacia, apricot and mulberry will also contribute to the shelter belts when the water comes, and smaller species of sand fixing vegetation and saplings are now being planted on a large scale. For the protection of young trees wind screens made of reeds have proved to be more satisfactory than solid ones. Impervious sheets hold back all the sand, and produce dunes before becoming buried. The setting up of the screens in sand is mechanised. Experiments are also in progress on the utilisation of a waste product from industry which, when sprayed on to sandy soil, will immobilise the surface, yet leave it permeable to rain and to vegetation.

There is much work connected with the irrigation of the desert which is of indirect biological importance. Seepage outward from canals is being checked by packing with clay, concrete or asphalt being prohibitively expensive. Intense rates of evaporation will lead not only to the loss of high percentages of the water entering the Turkmenian canal, but also to silt deposition and a tendency for the water to become saline. The silt content of the canal water is estimated to reach 20-25 million tons, and when deposited will be removed by electric excavators and suction dredgers, besides by silt eliminators such as those already in use in Uzbekistan. These are floating installations which, by stream directing shields, allow only pure water to enter a canal, thereby reducing the cost of cleaning out the canal to one tenth of its previous figure. Again a special centre, the All-Union Scientific Research Institute for Hydro-technique and Amelioration, is dealing with this work.

The other side of the scientific work concerns the productivity of the watered desert, and this is being prosecuted in laboratories as far apart as Moscow and Tash-

kent, and by field expeditions. Tashkent, for example, has been transformed during the last 30 years into a modern city by irrigation, by the utilisation of power, and by education. The Tashkent Academy of Sciences integrates the activities of 23 research institutes comprising about 1500 full time research workers who are additional to those working in the University, and most of them are of the Uzbek and other Asian races.

A soil survey is being made in considerable detail. Shifting sand has in parts smothered fertile desert soils which are being reclaimed. A detailed knowledge of the soil and subsoil is necessary both for the choice of the most suitable crop plants, and for the decisions concerning methods of improving difficult types of soil. Research stations are engaged on these problems. For example the clay plain north of Kizyl-Arvat and patches of clay on the route of the canal were once considered unsuitable for cultivation. Studies on the chemical and physical properties of these peculiar soils has shown that when the texture can be improved they become fertile.

The areas to be watered by periodic flooding are greater than those to be irrigated. Agronomists from the Institute for the Amelioration of Water and Marshes Economy are selecting suitable grasses for growing on the new pastures, and the plant breeding stations are taking steps to produce the seed in quantity. There are now 72 plant breeding stations with 4,000 to 5,000 acres each, situated in different parts of the Soviet Union. The animal breeders are endeavouring to improve the stocks of Karakul sheep to graze these new meadows, and Turkmenian Tekin horses are already of high quality. Increase in cattle is being prosecuted by careful breeding and by modern methods, and improvement in agricultural methods of fodder crop production. The natural supply of fertilisers occurring in parts of the Turkmenian desert are being exploited in increasing quantity, fertilisers are added every six weeks for some plants, and seven crops of lucerne, for example, are being harvested each year by these methods.

The mechanisation of desert agriculture and the production of suitable varieties of economic plants have made great strides in recent years. Problems of drainage are being attended to, and are equal in importance to those of irrigation because increases in soil salinity must be avoided. Yields of cotton per acre had trebled since 1932 in the fields which I visited. The Tashkent cotton institute for example, employs more than 40 scientists and over 200 other workers. Varieties of cotton suited to certain localities are produced by hybridisation and by other means. A pre-sowing treatment of the seed is providing a method of obtaining plants which are more resistant to saline soils, and much of the desert which will be watered is saline. Two crops a year can be harvested, and up to 30 cwt. of cotton per acre can be raised in the irrigated parts of Turkmenia. Two crops of wheat a year are also practicable. The plant breeding stations near Ashkhabad and at Kara-Kala and Kara-Kalinskaya are engaged in producing subtropical fruits suitable for cultivation in the areas to be irrigated, and large scale production of cherry, apricot and peach trees is going ahead for planting on the present arid wastes of Turkmenia. The Uzbekistan stations have already accomplished much in the production of locally suitable varieties of hard fruit which I saw cropping heavily. The first 5,000 acres of new land were irrigated in 1952 and on it experimental crops are being grown.

In the summer of 1951 there were 22 expeditions of botanists, zoologists and soil workers distributed in the Kara Kum desert, and a party of zoologists from the Turkmenian Academy of Sciences has travelled about 2500 miles in the valleys of the Atrek, Sumbar and Chandir rivers. I discussed the work of these parties with some of their members and saw some of their material being worked upon in their laboratories. An intensive 2 years of field work has preceded the actual building of desert dams and canals, in the same way that the data collected by the pre-war scientific expeditions to the region between the Volga and the Ural rivers has been utilised in planning the irrigation in progress there. Each group working in the Kara Kum desert comprised 12 to 20 persons coming from all over the Soviet Union, besides from the young academies of sciences and universities of the central Asian states.

Seeds of certain plants which are wanted for the new pastures and meadows were being collected, and surveys were being made of the native plants and animals. A look-out is always kept for wild varieties that can be turned to economic use, as were the rubber bearing *Scorzonera tau-saghys* and *Taraxacum kok-saghys*, 'dandelions' found in the Tien Shan mountains in 1930 and 1931. These two species now provide the major part of the rubber crop of the U.S.S.R.

Ecological studies are stressed, and detailed work is carried on in selected places, both virgin and in the oases. A few semi-permanent desert laboratories have been set up for this work and for the soil analysis. I saw many cultures of soil micro-organisms maintained in the Institute of Zoology at Tashkent.

A large field of work before the expeditions and the laboratory workers concerns parasites and pests in general. The normal pests and predators of desert trees, shrubs and plants which are about to be grown on a large scale are being studied, rodents as well as insects, so that any enormous increase in the numbers of these organisms arising from the altered balance of nature may be dealt with immediately by appropriate measures, and wholesale destruction avoided.

Predators and parasites of domestic or potentially domestic animals are being investigated, and every opportunity is being taken to follow out the life cycles of flatworms and other parasites which inhabit two or more hosts. Information is being collected concerning the species and habits of molluscan and other intermediate hosts. The work associated with insect vectors of diseases of all kinds is as important here as in other warm countries, and employs many persons. The incidence of malaria in the oases is now low; I myself saw no mosquitos and I did not use the nets with which I was provided. All slowly flowing irrigation channels dry out completely between flooding which takes place every twelfth day for cotton. Gad-fly problems, they told me, had been satisfactorily solved. Physiological work on domestic mammals occupies many workers.

The most important crop to be raised in Turkmenia will be cotton, with much wheat, rice, dates, olives, fruit and plants producing rubber and essential oils. Cotton and rice will also be grown in the Ukraine for the first time. The anticipated yields from the whole of the new irrigation schemes include, in millions of tons: wheat 8, sugar beet 6, cotton 3, rice ½, together with 2 million head of cattle and 9 million head of sheep. This represents food for a 100 million persons, besides the industrial crops.

The deflection of so much water on to the land by the dam being built on the Amu Darya river to supply the Turkmenian canal will inevitably lead to a lowering in level of the Aral sea, and an increase in its salinity. This is welcomed up to a point because a reduction in subsoil water levels will make available large tracts of the fertile delta of the Amu Darya for cultivation. The Caspian Sea will in time also be affected by the diversion of so much water from the Volga on to the land.

The effects of irrigation of the new areas, which are equal to one-third of the world's irrigated land, will also be to better the climate over an area estimated at some 300 million acres (an area larger than that of Europe), the temperatures will become less extreme and the atmosphere more humid. The probable details of the climatic effects of the schemes and the future water balance of the inland seas are the subjects of much discussion in the Soviet Union.

The realisation of projects of this kind, which in scale approach those of natural forces, is being carried out by mechanised navvying. In five to seven years about 4,000 million cubic yards of earth are being shifted – this represents about sixteen times that moved for the Panama Canal – 25 million cubic yards of concrete are being mixed, and thousands of tons of metal sections and equipment are being used. A labour force of 200,000 persons is operating the machines for this work. Drag-line excavators employ buckets of 18 to 32 cubic yards capacity, and their load can be dug and dumped 130 yards away in a minute. Suction dredgers, having piled up the earth wings to the Tsimlyanskaya dam on the Don, are now in use in the Amu Darya. Each unit is manned by 10 engineers and it can operate down to a depth of 70 feet, churning earth to a suction head from which it is removed by pipe for distances up to 3 miles, and doing the work equivalent to about 10,000 to 15,000 men provided with picks and shovels. Automatically controlled concrete mixing combines and many other machines have been specially designed for the developmental schemes. Routes of communication are being developed, new towns are growing up and are being staked out in the desert ready to receive the water when it comes in 1957. Krasnovodsk, at the Caspian end of the canal, was once a desolate waterless place.; it is now a beautiful modern city with an abundance of greenery, as in Tashkent.

This wide control over factors which limit life, and the productive development of a large part of the potentially fertile central Asian deserts has been made possible by detailed preliminary planning and by research of many kinds, ranging from purely biological problems to such matters as the properties of alloys and methods of constructing dams which will ride earthquakes and not be destroyed by them (as are needed in western Turkmenia). All these things are just as necessary as an ability to meet the scale of the engineering requirements. But above all, it is the integration of the many lines of work, directly of a biological nature and indirectly of biological significance, that is leading to such immense productivity within a few years.

Only two great rivers traverse these Asian deserts; the Syr Darya is already used almost to capacity for irrigation in Uzbekistan, and the Amu Darya, with an annual flow of 10 and a half cubic miles, is being diverted in part across Turkmenia to water 20 of the 37 million acres of potentially productive land. Long term projects are now being planned for the diversion of some 70 cubic miles of water annually from the

northwardly flowing Siberian rivers. Dams, canals and dried up river beds could carry this water 2,500 miles to central Asia, and this would make possible the irrigation of some 62 million acres of land for crops and 87 million acres for pasture, so satisfying all central Asian needs for water. The more humid atmosphere would bring milder winters which would allow agriculture to be carried out further north than is at present possible. These projects could be started after 1957 when the Turkmenian canal is to be finished, and the central Asian states could then support a population of 120 million instead of the present 20 millions. Modern civilisation could inhabit the sites of ancient communities, abandoned when the water supplies disappeared.

ASPECTS OF THE ECOLOGY AND PRODUCTIVITY OF SOME OF THE MORE ARID REGIONS OF SOUTHERN AND EASTERN AFRICA

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I *Introductory Remarks.*

As the purpose of the symposium is to study features of the ecology and productivity of *deserts* it could, with justice, be asked why I should deal with regions and phenomena that, for the greater part, fall outside the conception and definition of the *desert proper.*

II *Objects.*

My objects are:-

(1) To discuss briefly a few selected climatic regions of *desert, sub-desert, arid* and *sub-arid* nature in relation to their actual and possible usefulness and the threat of desiccation to which they are exposed.

(2) To touch on some of the ecological phenomena and problems in such regions.

(3) To record some of the major factors, processes and agencies presenting problems in the control of desiccation.

(4) To suggest ways and means of improving the productivity of some of the regions simultaneously with the control of the march of 'desertification'.

My reasons are these: Even if we accept the view that climatically the whole or portions of Africa and adjacent regions of Southern Europe, Persia and Arabia, during more recent geological time, have little or no tendency toward increasing aridity and that there is likely to be but slight change in this direction in the coming tens of millions of years, we dare not close our eyes to the portents of a man-induced desiccation or 'desertification' associated with the *more arid* if not truly *desert* regions of Africa. More cogent even is an attempt to interpret the shape of things to come if we accept as a working hypothesis that we are experiencing today the ushering in of a phase of progressive aridity. If we agree with le Danois (1950) that on a world wide scale deserts have increased within the past 3000 to 5000 years – and more particularly in the relevant regions of Asia, Eastern Europe and Africa – and that the sands are driving into drier but not yet desert regions adjacent, there is all the more reason for an emphasis upon the potentials and problems of the regions facing growing danger of desiccation.

III *Some of the Major More Arid Regions.*

In the regions listed below serious local erosion and desiccation problems exist, which, if not solved within reasonable time, are likely to increase the man-made desert.

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In a fuller account of the regions to be published elsewhere I refer briefly to the major features of vegetation, productivity actual and potential, and the nature of the threat already evident as the outcome of man's action.

(1) The Namib and the Great Nama Land *Deserts*
 (i) The Namib
 (ii) The Great Nama Land Desert.

(2) The *Sub-Deserts* of the Karroo and the Kalahari
 (i) The Karroo
 (ii) The Sub-Desert Kalahari.

(3) Certain Dry Tropical/Sub-Tropical Regions of Southern and Eastern Africa
 (i) Arid Regions
  (a) Arid portions of the North-Central Cape Province, South-Western and Western Orange Free State and Extreme Western Transvaal.
  (b) The Arid Kalahari
  (c) The Arid Limpopo Region
  (d) Arid Portions of North-Eastern Tanganyika and South East Kenya together with Arid country linking with the 'Somali' Region to the North
  (e) The Arid 'Somali' Region.
 (ii) Sub-Arid Regions
  (a) The sub-arid Bushveld of the Transvaal
  (b) Sub-arid regions in Northern Bechuanaland and Southern Rhodesia
  (c) Sub-arid portions of Central Tanganyika
   (i) Tribal Agriculture
   (ii) East African Groundnuts Scheme: Kongwa Region.
 (iii) Semi-Sub-Arid Regions.

IV *Some Ecological Phenomena and Problems.*

In the fuller record to be published elsewhere I deal briefly with the following ecological phenomena and problems:-

(1) Habitat Factors
 (i) Radiation
 (ii) Humidity
 (iii) Evaporation
 (iv) Dew
 (v) Rainfall
 (vi) Edaphic factors.

(2) Biological and Ecological Phenomena
 (i) Succession and development
 (ii) Community and climax
 (iii) Physiological and aut-ecological investigations
 (iv) Physiology and reactions of animals
 (v) The role of fire.

V *Productivity Actual and Potential of the Desert and Other Dry Regions Together with some of the Problems Involved.*

(1) Productivity.

(i) The *deserts* are of no actual and potential productive value, except very locally for light browsing by nomadic to semi-nomadic hardy sheep and goats based on drinking points and except for very limited irrigation of suitable soils. The Namib is of much less value than the Great Nama Land Desert for browse, local as this is even in the last named region.

For reasons of protection of adjacent regions of greater value the conservation of the deserts, toward their margins is essential.

(ii) The *sub-deserts* Karroo and Kalahari are of value for grazing and browsing. In the Karroo steady and widespread deterioration has followed the mismanagement of the browse land, presenting a national problem. Nothing less than a combined individual and national effort to reclaim the Karroo veld can save this region from desolation, a desolation that would have disastrous effects on regions adjacent because of the eastward and northward march of the sub-desert. Local irrigation is actual and potential, but demands much care in the use of water.

(iii) The *arid* regions are in imminent danger of increasing desiccation as the outcome of mismanagement of livestock. These regions are of little crop production value, apart from local peasant field husbandry, which demands constant direction if its deteriorating influence is to be avoided.

(iv) The *sub-arid* region of the Transvaal Bushveld is in imminent danger due to mismanagement of the natural grazing. Arising from the same cause, there are marked signals of distress in portions of Central Tanganyika.

African peasant arable agriculture in Central Tanganyika requires particular guidance and the continued insistence on conservation measures if the growing deterioration of portions of the country is to be stemmed in time.

(2) Some of the Problems Involved.

Matters of far-reaching significance in the maintenance and the development of productivity in the *arid* and *sub-arid* regions are:-

(i) Where Tsetse-fly still exists on a large scale its attempted removal and the efforts to introduce livestock to fly-free areas must be accompanied by a policy and practice of herd control and pasture management, supply of water points, conservation farming and informed and firm administrative direction of the local people. Particularly disastrous is the consequence of uncontrolled continuance of the widespread 'lobola' or purchasing of wives by means of thriftless livestock – the status of a man being judged not by quality of his livestock but by the number. In 1928 I sounded the note to the Governor of Tanganyika of the day that because no government in Africa at that time appeared prepared to shoulder these necessary controlling responsibilities the 'fly' should be considered as the guardian of

much of the continent – against the ravages of erosion and desiccation. I have since, on several occasions, reiterated the same thought. In the absence of measures providing for the conservation of country hitherto under 'fly', overstocking would readily produce a far worse curse than the 'fly': additional foci of desiccation. It is heartening to read that recently the tribesmen in Sukumaland, Lake Province, have accepted a plan for the reduction of their stock by culling. If successful and if applied generally this may have far-reaching influences on wise use of land freed of 'fly'.

Again I make a plea for the planned freeing of all such country from the 'fly' and its appropriate use and conservation on an organized basis.

(ii) Solution of the problems of economic and acceptable livestock reduction and of the management of natural pastures in the drier portions under review, is made all the more urgent because of the marked influence of selective grazing and browsing and the witholding of fire upon the rapid establishment of vast areas of thorny and other thicket and scrub, in which Acacia and Dichrostachys frequently play a role. Millions of acres in South, Central and East Africa are either in or advancing toward this condition – its sole merit being that its impenetrability renders the ground it covers safe from further trampling by livestock.

Measures for the rehabilitation of such areas, by means of scrub and thicket thinning and removal accompanied by protection for a time and, later, by systematic management of grazing, must be introduced if vast acreages are not to be permanently lost to the use of man – otherwise a desert due to erosion would be replaced by one of thorns!

(iii) Large-scale enterprises aiming at the ranching of the *arid* and *semi-arid* regions, where such are Tsetse-free, will succeed to the degree to which those responsible undertake rational preliminary survey of the potentialities, the provision of adequately distributed water points, the management of the natural grazing and browse, the setting aside of reserve grazing or fodder against hazard of drought and the consistent giving of attention to pests and diseases.

Considerable potential there is in the Kalahari and in parts of Rhodesia and Tanganyika for enterprises of the right kind properly planned and directed. Hasty, ill-directed action would end in disaster.

(iv) In the *sub-arid* regions – notably in Rhodesia and Tanganyika, *large-scale mechanized* crop production should not be attempted, no matter how encouraging the temporary successes on the now small-scaled scheme at Kongwa or elsewhere in similar country may appear. The costs of clearing of vegetation, the preparation of the land and of periodic losses due to serious droughts would not be justified. Nevertheless, it remains true that on lower lying, alluvial soil within the sub-arid areas small scale mechanized production of Groundnuts and Sorghum may be economically worth while. In such areas Maize should normally be considered uncertain, owing to the marginal nature of the regions in terms of rainfall reliability.

(v) Selection and breeding of suitable exceptionally drought-hardy varieties, particularly of Sorghum, Maize, Groundnuts and other legumes as well as of Cotton, require consistent attention. Promising indications have been yielded as the result of investigations in various of the drier regional centres in South Africa.

VI *The future.*

It would be easy to prepare programmes for survey, research and administrative action and to suggest resolutions for this Conference, drawing the attention of the various Governments to the problems and threats already well known. This would be a repetition of what has been covered in varying degree fairly recently at such official gatherings as: the First Commonwealth Conference on Tropical and Sub-tropical Soils (Harpenden 1948), which was attended also by representatives of certain non-Commonwealth countries, the African Soils Conference (Goma, 1948) and the African Regional Scientific Conference (Johannesburg, 1949). In addition, the creation of the Inter-African Information Bureau for Soil Conservation and Land Utilization, in Paris, as the outcome of the Goma Conference (African Soils, 1951), the setting up of the Council for Scientific Research in Africa South of the Sahara and the establishment by U.N.E.S.C.O. of the International Arid Zone Research Council – which in turn has appointed a standing Advisory Committee on Arid Zone Research – augur well for the provision of the requisite scientific, applied economic and administrative information regarding all aspects of the threats of desiccation.

The selection by the above mentioned standing Advisory Committee on Arid Zone Research of the two centres in Algeria – The Saharan Research Centre at Beni-Abbes Oasis on the Qued Saoura in the Southern Algerian Territories, and the Beni Ouif Saharan Biology Station in the Sud Ouranais midway between Colomb Bechar and Ain Sefra – is an advance.

On the applied and economic sides the French are engaged in agricultural, conservation and other work in several of the desert, semi-desert and arid regions of their North and West African Empire.

A survey of action being taken in the territories mentioned reveals that the Union of South Africa and Southern Rhodesia have special legislation and services for combat of the causes and retardation of the processes of desiccation, while to a lesser degree provision has been made in the British Colonial Territories such as Northern Rhodesia, Nyassaland, Tanganyika, Kenya and British Somaliland. The Portuguese have commenced in Mozambique, while for a part of Somalia there has been a survey of aspects of the problem by a recent F.A.O. Mission.

From this it might be argued that all is well, that the authorities are aware of the need for appropriate action and that such is indeed being either taken or seriously planned.

Unfortunately, the scope and the degree of practical action does not fit the dangers facing us. In part this is due to shortage of funds but rather more because of the lack of staff with the necessary training and experience, while the want of

machinery and equipment is also a serious handicap. Beyond all this, however, are the powerful forces of inertia on the part of the agricultural communities, European and African, who fail to realise the seriousness of the situation.

Though counsels of perfection may appear, it is necessary to emphasize the following once again to Governments and peoples.

(1) Magnitude of the dangers threatening us all.

(2) Need for more vigorous propaganda and education of all kinds and in all circles from ploughman to parliamentarian.

(3) Urgency of training many more men at the various levels for undertaking work of various kinds – scientific and other – against the menaces emerging from current agricultural and related practices.

(4) The absolute necessity for attracting more men for the planning of reclamation, conservation and rational land use – notwithstanding the increased national expenditure involved in the offering of better stipends and careers.

(5) Close and frequent collaboration among the various States, so that matters of policy and practice may be the more readily studied and co-ordinated action the more readily taken.

In retelling what is already known we must remember – in our endeavours in any great matter – the sentiment that '. . . it is not the beginning, but the *continuing* of the same, until it be thoroughly finished, which yieldeth the true glory . . .' We must *continue* advising, guiding, stimulation and educating to the uttermost.

Meanwhile the desert is on the march. We must act so that this march does not end in the 'Great South (– Central – Eastern –) African Desert uninhabitable by man'. (Drought Investigation Commission, S.A. 1923 – except for the words within brackets!)

PROBLEMS OF PHYSIOLOGY AND ECOLOGY OF DESERT ANIMALS

Professor F. S. Bodenheimer

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The endocrine cycle of the reproductive glands in desert animals.

In all climates manifesting distinct seasonal contrasts the majority of terrestrial vertebrates undergo a conspicuous annual cycle with regard to the seasonal activity and the histological structure of the endocrine glands, especially of the gonads. These seasonal changes occur in response to changes of external stimuli, such as temperature, humidity, duration of day, etc., and their effect always results in the birth of the young at the season of the most luscious vegetation. Accordingly, the rutting season is usually in the climatic autumn, and that of birth in the climatic spring. This synchronization of the reproductive cycles into annual cycles of climate and vegetation is doubtless of the greatest ecological importance. It is such a conspicuous phenomenon that it can scarcely be overlooked. In many cases this synchronization is fixed by heredity and is more or less rigid at least so long as no counteracting external stimuli change the normal cycle. Thus we know that sheep or deer transported from a moderate climate in the northern hemisphere to a corresponding one in the southern hemisphere, where the winter corresponds to the northern summer, adapt themselves within one or two seasons to the climatic cycle of the new environment. Yet for the camel a transfer into the summer-rain regions of the Sudan means an experiment which is rarely survived and still more rarely leads to reproduction within the Sudanese cycle of precipitation.

The habitual seasonal cycle of reproduction is however often maintained for a long time in a not entirely different climate where only the normal releasing external stimuli are missing. Major Flower has published birth data for a number of species of gazelles normally living in rather varied climatic conditions in N. E. Africa, which with their offspring were kept for a long time in the Cairo Zoo. In Cairo rain is practically absent. Fresh berseem-clover or lucerne (produced by irrigation) is fed to the animals throughout the year, and the *trend* of temperature and of day-length is more or less identical with that in their home countries. He showed that the monthly birth incidence of gazelles in the Cairo Zoo remained for many years, in full agreement with the seasonal rain cycles of their native regions, the peak of the births usually following that of the rains by one month. The only typical domestic animal of our deserts is the camel, whose reproductive endocrine cycle has recently been studied in the Negeb, S. Israel, by R. Volcani. The camel, in contrast to many other domestic animals, has preserved a pronounced rutting season from January to March. Its pregnancy lasts 12 months, suckling 3 to 4 months, and the interval between births is two years. Both birth and rutting seasons coincide with the season of luxuriant vegetation on the margins of the desert. This is an extreme and most remarkable adaptation to the desert environment with its short period of green vegetation. In consequence reproduction occurs only once in two years.

During the rutting season the female is 'on heat' for periods of 7 days with 20-day intervals, until fertilization has taken place. The seasonal changes of the

ovary could not be followed, as females are not slaughtered at the age of fertility. In the male, however, the testes and the epididymis show the following changes:

Month	Testes		Epididymis	
	Weight (grams)	Activity (1-4)	Weight (grams)	Sperm in lumen (1-5)
V-VII	66	1.0	17	0.7
VIII-X	91	2.5	24	1.8
XI-XII	70	4.0	16	3.0
II-III		4.0		4.5
IV	96	1.5	25	1.0

The peak in the weight of the testes in autumn does not have the same significance. The peak of 96 g in February-March is connected with the rutting season, whilst that of 91 g in August-October is due to heavy hydration. During December-March the diameter of the tubules is 183μ with 5-6 layers of germ cells in various stages of differentiation with abundant mitoses. Many sperms are seen between the Sartoli cells, their tails directed towards the lumen. The walls of the tubules are highly acidophilous. The space between them is narrow, and their walls often touch those of neighbouring tubules. The intersitial tissue is compressed, and its nuclei are stained a dark colour by haematoxylin.

From March onwards, degeneration sets in; more and more of the tubules are devoid of sperms and vacuolization becomes conspicuous. In May this degeneration is well advanced; a few wall layers only are seen in the tubules and these are often reduced to one. Sperms are almost absent, as are mitoses. The diameter of the tubules is reduced to 131μ, and the interstitial tissue is loose. In October, rejuvenation of the germ cells begins simultaneously with the disappearance of the degenerated cells. The diameter of the tubules slowly increases, and an ever increasing number of sperms is observed. From November to January, rejuvenation progresses, reaching its annual peak in February. Observations on the epididymis and the presence of sperms within its lumen agree with the seasonal trend of the testes. The thyroid shows colloidal accumulation in extending lumina from July to November. Until February the cells remain flat, the nuclei are at rest and no further secretion is observed. During February the cells of the glands become columnar and their nuclei are reduced. From March and April onward, a slow preparatory accumulation of colloidal secretion into the lumen begins. The seasonal peak of the thyroid closely follows that of the testes.

The reproductive season of many species of small rodents in the desert also seems to be concentrated in the short climatic spring, although prolonged breedings of *Meriones, Acomys,* etc. have shown that under suitable environmental conditions they are able to continue reproduction throughout the year. The limiting factor seems to be the composition of the food. We have shown for *Microtus* that in Israel, certain factors in green plants may induce a duplication of fertility by raising the number of eggs per ovulation, as well as by shortening the interval between two consecutive pregnancies. *Microtus* is apparently unable to maintain fertility on a

diet of dry vegetation alone. Prolonged droughts bring it to the margin of total extermination, except in certain favourable localities like the borders of swamps, irrigated fields, etc. In the typical desert rodents either the normal rate of ecological destruction or the physiological resistance to dry food (largely replaced in the desert by bulbs and succulent plants) must differ considerably from that of *Microtus*, which is prevented from entering the desert at all. The seasonal and annual fluctuations of the populations of the nocturnal desert mammals have not been studied. Their enemies may be few, for there are not many nocturnal birds of prey, although snakes are abundant.

The seasonal reproductive cycle of desert birds usually differs from that of the birds of neighbouring regions. Most of our desert birds breed rather early (mainly in March) according to the rainfall, and breeding ends in late March. The desert offers sufficient food for the rearing of young only during the short period of late winter vegetation. The total number of eggs and of broods per female per year is reduced as compared with that in more favourable biotopes. Thus *Oenanthe lugens* only has up to 5, compared with the 42 eggs of the equal sized *Erythropygia* in Mediterranean territory. The great heat reduces the size of the hunting area, and still more important, it enforces upon desert birds many hours of additional rest at noon. The energy spent in finding the same amount of food is also much greater than in more favoured biotopes. These observations easily explain the lack of attraction which the desert even at its most favourable season, exerts upon hibernating, aestivating or resident birds beyond its borders. On the other hand, Heim de Balzac observed that on the southern borders of the Sahara, a number of resident birds extend their breeding area into the savanna, far beyond the limits of the desert vegetation. We must assume that in that season only are conditions favourable for them in the savanna. Mobile birds are able to utilize this situation for extending their range during the short but vital season of nidification and reproduction, when the food situation is less favourable in their permanent habitat, the true desert.

In reptiles a seasonal cycle of the gonads is also observed. Here the seasonal occurrence of the main items of food as well as the historic origin of every species are of importance. Whilst reptile-eating species may reproduce late in the season, insectivorous reptiles breed early. The chamaeleon shows its historic affiliation with the African savanna from which it originates, by its reproduction late in autumn, when sycamore and charob trees are flowering. The reproduction of the few desert amphibians depends entirely upon the incidence of heavy precipitation.

Among small aquatic invertebrates as well as in the big Phyllopods (*Estheria*, etc.) a similar relation to rainfall prevails. The insects however show many parallels with the terrestrial vertebrates of the desert. Diapause in any stage from egg to mature adult, is one of the mechanisms of adaptation. It is induced and regulated by seasonal changes of the secretory glands in response to unfavourable stimuli. More attention should be paid to the secretory seasonal changes of the reproductive glands in desert animals, as well as to the analysis of the stimuli which induce these changes in every species.

Solar-radiation and colour pattern in desert animals.

In the bare and open desert landscape the intensity of solar-radiation, to which every diurnal animal is exposed is high even if it is often less than on bare mountains. For those animals that are active between late morning and late afternoon, this radiation is in summer of the highest ecological importance. It is surprising to find therefore, that no measurements are available on the transmission through the integrement of rays from ultra-violet to infra-red.

Three types of colour patterns are apparent in desert animals:-

(1) Mammals and birds show prevalently buff, sandy, pale grey or spotted colours and remain hidden during the day; or when they are diurnal, their chief enemies are nocturnal. Buxton, Heim de Balzac and Morrison-Scott have thoroughly destroyed the legend that this type of colouration is primarily protective*. We have to be satisfied with the statement that this 'adaptive' colouration is primarily a physiological effect of dry heat on the development of pigments.

(2) Many Orthoptera in particular, show a very intimate and complicated adaptation to the colour of the soil on which they live, imitating the pattern of the pebbles in their environment. Resting *Eremiaphila* and most *Acrididae* are usually not to be discerned even by a searching eye. They appear very conspicuous however immediately they fly. Here we obviously have some kind of appreciation of the colour of the environment immediately after the last moult via the eyes, the central nervous system and endocrine mechanisms (probably connected with the cardiac glands). A similar surprisingly close colour adaptation of the feathers exists in our common desert larks (*Ammomanes* spp.), as well as in some other desert birds.

(3) The high proportion of black colouration in diurnal desert animals, was apparently first pointed out by Buxton. This is a rather puzzling phenomenon, as it seems to be a bad adaptation for desert animals and increases the absorption of heat. Some of these black desert animals have black colouration in other biotopes too, so that their blackness is no adaptation; but this only raises the question why black elements prevail so much amongst the diurnal desert animals. Among those are the Tenebrionid beetles which predominate in most deserts of which the nocturnal species (*Blaps*) are not less black than are the more common diurnal species. The same can be claimed for the ravens, except that our desert ravens have perhaps a less deep black nuance than have their cousins beyond the deserts. In both these cases black is the common ancestral colour of the group. Wheatears and chats (*Oenanthe, Saxicola*) are another group of prevalently black desert birds. Buxton points out that their transformation from a buff to a black and white pattern can easily be followed. Here we have apparently a definite adaptation to the desert. The same is true for a number of insects such as the blackish races of *Metacerus* and other grasshoppers.

We may also refer to an analogous condition in man. The tents of the Bedouins of the desert are usually black (or dark brown) and their thick overcoats or abbayas

* c.f. Cott, H. B. 1940. *Adaptive coloration in animals.* London, p. 154 – Ed.

show the same colour. This empirical choice certainly has its reasons which we are at present unable to recognise. It should also be pointed out that for all diurnal terrestrial animals of the desert the strong radiation from the soil is an important ecological factor. Their black colour may be the consequence of raised melanin production as a reaction to certain parts of the solar spectrum, just as melanin is increased by higher metabolic activity. The latter has been experimentally demonstrated in the phases of the Desert Locust (*Schistocerca gregaria*), where the black colour of the gregarious hoppers contrasts with the pale green of the hoppers of the solitary phase. Superimposed on the effect of raised activity is the effect of the hours of sun basking (i.e. of intensive exposure to solar radiation) which are greatly prolonged, especially in the first stages of the gregarious hoppers as compared with the solitary ones. Another mechanism produces adaptive black colouration among the animals found in areas of black lava, (e.g. *Agama stelliopicae*), or on burnt or otherwise blackish soil (as in many grasshoppers).

Of special interest is an internal black pigmentation in the peritoneum and pleura of desert reptiles. Alpine climatologists stated some decades ago that alpine lizards (*Lacerta* spp.) show black pigmentation of this kind. We have just begun to pay attention to this phenomenon in our region, and we find it to be of common occurrence in lizards with diurnal summer activity, such as *Acanthodactylus, Lacerta, Agama, Eremias,* etc. The deepest, velvet-black pigmentation of this type occurs in the chameleon, which is especially exposed to sun radiation. In some species, even the omentum and its fat show patches of black pigment. Before speculating about these phenomena we must have information as to whether black pigmentation is common to lizards and snakes in more northern climates. Some English species, *Lacerta vivipara* and *L. agilis* possess a black peritoneum, whilst *Anguis fragilis, Vipera berus* and *Natrix natrix* do not. The long exposure to strong solar radiation of all diurnal desert animals between spring and autumn raises a number of questions of physical physiology. The first and most important of these is to what degree the rays of various wave-length in the solar spectrum are able to pierce the dead part of the integument. We therefore undertook (in co-operation with Drs Halperin and Svirski) some preliminary measurements on the transmission of rays through the integument of freshly killed insects and reptiles. The experiments were conducted with a Beckman Quartz spectrophotometer. The results indicated that the actual quantity of transmission depends primarily upon the intensity of the radiation. Through the transparent wings of a dragonfly (*Crocothemis*) transmission in all ranges of the spectrum is very high, even higher than for normal glass. Yet through all other objects transmission in the ultra-violet range is nil, except perhaps for a slight transmission through the white-scaled forewings of *Pieris rapae*.. Some slight transmission is always observed in the higher range of the visible spectrum, whilst transmission is always important in the infra-red range, where in all cases it reached a maximum at 1200μ. This applied also to black insects. In the reptiles we had expected some ultra-violet transmission as we had regarded the black pigmentation of the integument as a reaction against it. Instead, transmission of ultra-violet through the skin of back and belly of *Ophisops elegans* and two other lizards (*Chalcides* and *Eumenes*) was found to be absolutely nil. It was very low in the visible part of

the spectrum, and was least of all in the infra-red. The protection of the tissues of the reptile body by the corneous part of the integument against penetration of any kind of solar radiation is thus extremely efficient.

These measurements were made with the subject under investigation near the exit slit of the spectrophotometer, at a distance of 4.5 cm from the window of the phototube. In a second series the subjects were placed much closer to the phototube (1 cm distance). The ray that reached the object was thus much more concentrated. In consequence all readings gave higher transmission (up to 100%), but the general picture remained the same. The readings in this second series gave approximately maximum values at right-angle incidence to the rays, which in nature would be an extremely unusual occurrence. The first series is certainly a better illustration of what actually occurs in nature. Absorption of heat at the actual angles of ray-incidence may be even lower than in the first series. The peak of transmission at 1200μ in all the objects tested led to a further exploration of the 1000 to 14000μ region, using Beckman I. R. 2 (sodium chloride optical apparatus). These results show a second peak at 5400μ and deep depressions at 3000 and 6000μ. The first of these may be produced by an *OH*-bond; the second may be due to the presence of water.

From the results of the experiments it is perfectly clear, that the fur and feathers of mammals and birds are quite sufficient to prevent any transmission of the ultra-violet and visible rays of the solar spectrum to the integument. The degree of transmission in the infra-red, low as it probably is, deserves further study. Yet these qualities of fur and feathers are certainly no special adaptation of desert animals, but hold good for mammals and birds in all biotopes.

The study of these problems is still very much at its beginning. The physiological consequences of the colour and structure of the integument, the importance of the angle at which radiation meets the integument, etc. need much detailed research. One point only is clear: the integument is normally fairly well protected against penetration into its living tissues, irrespective of colour. For the time being we would stress not the differences observed in our various objects, but the striking similarity in the transmission trend through all colours and integumental structures. The two peaks of transmission at 1200 and 5400μ, and the two depressions at 3000 and 6000μ, as well as the general non-transmittance of ultra-violet rays are probably due to certain biochemical components common to the integuments of all animals.

DOMESTICATED ANIMALS INHABITING DESERT AREAS

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I do not think I need apologise for limiting my paper to *domesticated* animals, for such animals are essential to the economy of the human populations inhabiting desert areas; they provide milk (often the only form of liquid available for human consumption) ghee and cheese, meat, hides and skins for clothing, hair for tents and other purposes, means of human and baggage transport, and even fuel in the form of dried dung. These products are provided not only in sufficient quantity to meet the local population's own needs, but are frequently available for export from the desert areas. In spite of this, textbooks on animal ecology have almost without exception failed to devote more than an occasional paragraph or two to domesticated animals, and particularly to those inhabiting desert areas, while little work has been done on the physiological reactions of such animals to their environments. This applies equally to practically all classes of desert stock, – not merely to camels but to fat-tailed and fat-rumped sheep, goats, yaks and donkeys. Our largest body of knowledge is in fact on cattle, which are not typical desert animals, though they are of course widely found in the semi-arid areas bordering on deserts, such as East and Central Africa and Northern India. For this reason I have not hesitated to draw on cattle for certain illustrative material in this paper.

The effects of climate on the morphology of desert animals may be roughly classed as *direct* and *indirect*. The *direct* effects are associated with environmental temperature (including solar radiation), with humidity, and with air movement. These can affect body size and conformation, the skin structure and nature of the coat covering, and possibly certain other properties (such as the subcutaneous fat layer) which may affect the absorption or dissipation of heat. The *indirect* effects are associated with the environmental vegetation and water supplies, and hence with the nutrition of the animal. These may to some extent affect size; they may affect conformation in so far as this is influenced by the local deposition of nutrient reserves designed to tide over rainless periods; they may affect the mechanism of food intake, and of water intake and conservation; and they may be related to the animal's facility for speed of movement.

It will therefore be desirable to summarise briefly the climatic environments to which domesticated desert animals need to be adapted. Since such animals are too large to avoid the extremes of climate in ways which are possible for smaller mammals (e.g. by burrowing) it is necessary to take into account the full climatic environment of the open desert. For this purpose ordinary routine meteorological data, however inadequate, is the only source to draw on.

In sub-tropical and tropical deserts (such as the Sahara) the outstanding feature is the uniformly high temperature. As one goes north-east across the Great Palaearctic Desert region these *consistently* high temperatures are no longer found, but they are replaced by two characteristics, – by extreme seasonal variations and (particularly in the mid-regions at lower altitudes such as the Iraqi Desert) by

periods at extremely high temperatures, – exceeding in fact those of the tropical regions. These high temperatures are paralleled as one goes further north-east or as the elevation increases, by extremes of low temperature, – falling in the Iranian Plateau to freezing point, in the Turkestan Deserts to figures well below freezing point, and in the Gobi Desert of Mongolia to figures below *zero* degrees Fahrenheit. It is clear therefore that animals inhabiting desert regions must exhibit marked tolerance to heat, and in some areas, equally marked tolerance to cold. It is not, of course, possible to give strictly comparable figures for solar radiation, but they may be assumed to run roughly parallel with temperature.

Heat tolerance is, however, also affected by humidity, whether the animal loses heat by sweating, by transudation or by respiration. Variations in humidity are most conveniently shown by means of climographs, in which the dry bulb temperature is plotted against the relative humidity. From a study of such climographs, one would expect the need for heat tolerance to be low in the temperate areas of Europe; in a tropical desert like the Sahara there will need to be a high heat tolerance, but there will be opportunities for heat regulation by evaporative loss at the low relative humidities; in wet tropical areas, where high temperature and high humidity are combined, the dissipation of heat will however be especially difficult. Desert areas in intermediate climates show strikingly wide variations in environmental conditions, from hot dry in the summer months to cold wet in the winter; clearly the animals in such areas will have to possess wide adaptations to the *direct* effects of climate. It is perhaps relevant at this point to note that, while few reliable records of air movement are available, desert areas may normally be taken to involve free air movement, while wet tropical jungle conditions are usually characterised by relatively still air.

Turning to the *indirect* effects of climate (i.e. those concerned with vegetation and water supplies), these are best reflected in precipitation curves. Whether rainfall follows the continental or the Mediterranean pattern, the outstanding features of all desert areas are not merely their low *total* precipitation, but the long periods during which there is virtually a complete absence of rainfall, – extending for as much as six months out of the year. The only difference between semi-arid areas and the more typical desert areas is the higher total precipitation in the former during the rainy season, which will affect both the type of vegetation and the water resources. But all are characterized by long rainless periods, with consequent violent fluctuations in herbage growth and therefore in facilities for natural grazing.

May I turn now to actual illustrations of the climatic effects on animal morphology and adaptation. If in doing so I seem to rely too largely on teleological argument, I hope it will be realised that this is inevitable in view of our present meagre and non-quantitative knowledge of the subject.

The direct effects of climate on the *size* and *conformation* of animals have been summarized in Bergmann's and Allen's Rules. The former postulates a larger body size in the colder climates, – the effect of the larger body size being to reduce the surface area available for the dissipation of heat. The latter postulates a parallel lessening of the extremities in the colder climates. Put concisely, one would expect

a larger and more compact body in areas of low temperature, and a less compact body with longer limbs and greater surface area in hot climates. As regards *coat covering*, one would naturally expect a thicker coat – with correspondingly greater insulation – in colder than in warmer climates, though this may of course be affected by seasonal shedding.

These differences are well illustrated in the conformation and coat formation of sheep as one goes from the northern latitudes to the equator, i.e. as the environmental temperature increases. The Dorset Horn sheep is typical of our own temperate area. The body is of fair size, the conformation compact, the legs short, the neck stocky and the ears small. There is a thick and compact wool coat. This animal may be compared with the Kurdi sheep, typical of the Northern Iraq desert. Here the body is still of fair size and the coat ample, as would indeed be necessary during the cold seasons. But the legs are longer, the neck less stocky and the ears large, – a phenomenon which is incidentally paralleled in Hamilton's work on ear size in hares. The desert sheep of the tropics (for instance of Eritrea and the Sudan) illustrate the extreme development of these various features. The body is far less regular and compact, the legs exceptionally long, the neck elongated and the ears large. Moreover, there is now a complete change in the nature of the coat, which in place of wool consists of fine short hair, – a characteristic typical of sheep in all hot tropical regions of low elevation. I say 'of low elevation' because at higher altitudes (and therefore at lower environmental temperatures) this generalization no longer holds. The sheep of the Yeman plateau, which is at the same latitude as the Sudan, are not only woolled and otherwise comparable to those of the northern deserts, but are in fact virtually earless.

Closely comparable changes in conformation and coat thickness are found in desert goats. The Angora or Maraz goat – the origin of our Mohair supplies – which is found in Turkey and the extreme north of Iraq, is relatively compact, with shortish extremities, small ears, and a copious covering of fine hair. The Persian goat, still well coated, is somewhat longer limbed and longer eared, with a less compact body, – characteristics which are exaggerated (particularly as regards ear size) in the Syrian desert goat. Here again, however, there is a dramatic change in both form and coat in the tropical regions. As with the tropical desert sheep there is a marked elongation of the body and neck, the legs are characteristically lengthened, and the ears are almost uncomfortably large. Moreover the thicker coat of the northern type is again replaced by one of fine short hair.

Too much influence on length of leg should not, of course, be attributed to direct climatic effects; apart from other reasons, animals in desert areas are characteristically nomadic, and therefore require facilities for long and often relatively rapid movement. This is perhaps best illustrated (if I may break my sequence) in the length of leg of animals inhabiting northern deserts, – of which an excellent example is the wild ass of the Gobi Desert. Donkeys are the most important class of equines used by man in desert areas and their ability to cover long distances over waterless tracts is one of their greatest assets, – not unconnected, probably, with their origin

May I now turn to cattle, which though not primarily desert animals, are widely grazed nomadically in semi-arid areas. I should perhaps first refer to the Yak, which while not classed as true cattle, are close relatives and are typical of the cold Asiatic deserts of Mongolia and of the Tibetan plateau. This animal again shows all the characteristics of cold resistant types, with relatively heavy and compact body, small extremities and a thick insulating coat. The same may be said of our own temperate cattle as illustrated in the Highland and Galloway breeds. It is instructive to compare these with their counterpart in the tropical desert areas. Here, however, contrary to Davidson's findings for North America, Bergmann's rule regarding larger body size in cold areas no longer holds; cattle in desert and semi-arid areas are among the largest in the world. The explanation may well lie in the fact that, in such animals, the skin surface is very greatly increased by the abnormal development of the dewlap and, in the male, of the sheath. Both developments are paralleled by a marked increase in the fineness of the coat in comparison with temperate breeds. It would perhaps not be out of place to note at this point that the large size and exaggerated skin areas of the cattle of the hot deserts is not found in the hot but humid areas. Here the animals, while having normal sized extremities, are quite definitely dwarfed.

Although I have no personal experience of the colder Asiatic deserts, it appears that Bergmann's and Allen's rules are equally applicable to camels, – perhaps the best known desert animal. Thus the two-humped Bactrian camel, common to the cold deserts of Turkestan, is described as 'distinguished from its Arabian relative not only by the presence of two humps, but by the facts that it is heavier, more compact, and shorter in the leg, and that it has a heavier coat of longer hair'.

Camels form the obvious introduction to the second aspect of climate in relation to domesticated animals inhabiting desert areas, i.e. to the *indirect* effect of climate *via* the vegetation and water supplies. One minor but none the less important adaptation is that associated with the nature of the vegetation. Xerophyllous vegetation is notably hard and frequently spiked or thorny; yet the camel is able to derive its nutrients from such material which, indeed, forms an important part of its natural grazing. But the most striking feature of the camel, which makes it of special value as a true desert animal, is its ability to store a reserve of fat in the hump to provide energy (not water) to tide over rainless and therefore vegetationless periods.

This feature is not confined to camels; it is less widely recognized but probably more important from the aspect of desert utilization as a feature of fat-tailed and fat-rumped sheep. For some six months of the year deserts are (as I pointed out earlier) normally devoid of rain. During much of this period the surface of the desert is practically free from any vegetative growth. With the onset of the rains the whole picture is transformed by the growth of a thick carpet of annual herbage plants. The duration of this vegetation is, however, relatively short, and within a few weeks of the cessation of the rains it dries up and fragments, leaving only the sparsest supply of grazing nutrients for stock. Nevertheless, owing to the wide variations in the locality of rainfall, a flock may be able to secure more or less continuous grazing by constant movement across the desert – the basis of nomadism.

as fast movers and their remarkable ability to make good their water deficit by drinking at one time quantities which – weight for weight – would be impossible to man.

Reliance on a precarious rainfall does, however, involve the need for some form of adaptation which will furnish nomadic stock with a mobile reserve of food. While in the camel this is located in the hump, in the sheep it is located in the tail. The exact form of the tail varies with different types of sheep. In sheep inhabiting the northern deserts it usually consists of twin lobes, the upper surfaces of which form a continuation of the woolly coat; the under surface being bare of wool. In tropical sheep the tail is long, rather than wide and lobed, but is still capable of storing large quantities of fat. The tail of the fat-tailed sheep may, in the lush period, attain a weight of 15 lb. or more; in the lean period it will shrink to an empty bag or 'rope' of small proportions. It would not, I think, be out of place to draw attention to the fact that the existence of a fat-tail is in no way inimical to high productivity, as shown by the fine udder development and good mutton conformation of many desert sheep.

I have attempted in this paper to describe some of the more typical examples of the adaptations of domesticated animals inhabiting desert areas. I have done this with a two-fold object. First, I was anxious to stimulate interest in a field which has in the past been much neglected by zoologists and physiologists, and which not only merits increased attention on account of its economic importance but furnishes a mass of unsolved but intriguing problems. We are, for instance, still unaware of the factors influencing tolerance to wide variations in environmental temperature, apart from specific tolerances to heat and cold. And even in regard to the latter, substantial progress has only been made with cattle, and little or no work has been done on camels, fat-tailed sheep, goats and donkeys. We know little of the mechanism causing local fat deposition, or of the reasons for the wide variations in tail and rump pattern. These and many other problems provide wide scope for the research worker.

But my second reason for presenting the paper is that it justified, in my view, an extremely cautious approach to any proposals (and many have been made) to introduce into desert and semi-arid areas types of livestock which may *in their own environment* be more productive but which are unsuited either to the climate, the vegetation or the inevitable nomadic life of desert animals. I have indeed tried to show that the existing desert animals are themselves capable of quite outstanding production in spite of their harsh environment. If, as I firmly believe, such animals are destined to continue to play an essential role in the utilization of deserts, it will not be by their replacement by – or even their inter-breeding with – so-called 'improved' livestock. Rather must we look for improvement by the better selection among the indigenous animals themselves and by the partial alleviation of the desert environment, – through improvements in water supplies for stock in grazing areas, through the increased practice of semi-nomadism, and – where this is impracticable – through efforts to conserve fodder as an *external* reserve to reduce the demands on the *internal* reserves of the animal itself. By such means – and only by such means – can we hope not only to maintain but to increase the contribution of domesticated animals to the desert economy.

WATER CONSERVATION IN SMALL DESERT RODENTS

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Animals inhabiting deserts have in the course of evolution acquired morphological and physiological characteristics which enable them to live and thrive in an environment that is hostile and uninhabitable to other closely related forms.

Among rodents, specially adapted desert forms are found in all the major deserts around the world. It is interesting that these rodents, although they belong to different families are similarly adapted to their environment.

In the north American deserts the kangaroo rats and pocket mice (*Dipodomys* and *Perognathus*) of the family Heteromyidae are found. In the great Palaearctic desert we find *Gerbillus, Meriones* and *Dipodillus,* belonging to the family Muridae; and *Jaculus, Dipus* and *Alactaga* of the family Dipodidae. In South Africa, in the Kalahari desert, the rodent *Pedetes,* family Pedetidae, is found; and in the Australian deserts the family Muridae is represented by *Notomys.* All these rodents have several morphological features in common (Fig. 1) thus they are all adapted to a bipedal saltatorial life with elongated hindlegs and reduced number of toes. Several of them have cheek pockets (Heteromyidae) or gular pouch (*Notomys fuscus* and *cervinus*) and they all have greatly inflated bullae auditivae. They are nocturnal and stay in their underground burrows during the daytime.

Also with respect to their physiological adaptation to the environment do we find striking similarities between these animals.

Personally we have worked primarily with kangaroo rats (*Dipodomys*) but we have also had the opportunity to work with jerboas from Arabia and we found that their water problem has been solved in the same way as the kangaroo rats' has.

It seems likely that the same would be true of many other desert rodents.

Can the desert rodents live without water?

When we started to investigate the water metabolism of the kangaroo rats the first question to be answered was whether these animals can live entirely without drinking water. Previous reports in the literature indicated that this was the case but more accurate investigation was desirable to solve this problem. We kept kangaroo rats on diets of dry grain (rolled barley), without water. They maintained their body weight, and some even gained body weight over a period of 2 months.

The next question was: Can the animals during a period of water deprivation store their metabolic waste products to avoid spending water for excretion? This is practiced by the lungfish which stores urea in its body when estivating in the dry mud. The stored urea can amount to 2-4% of the body weight. Urea and electrolyte concentrations were determined in the plasma of (1) kangaroo rats that were freshly trapped, (2) kangaroo rats that had been on a moist diet (barley and watermelon) and (3) kangaroo rats that had been fed on dry barley only from 2-8 weeks. The same average urea and electrolyte concentration of the plasma was found in all

the groups and the concentrations were of the same order of magnitude as the concentrations found in other rodents, showing that there is no storage of waste products during water deprivation.

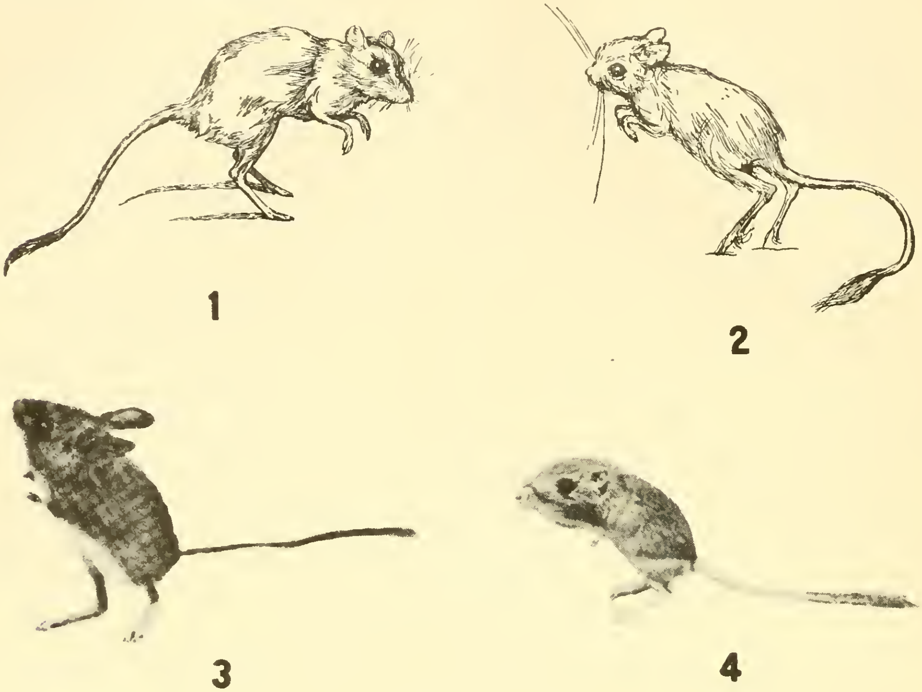

Figure 1.

Desert rodents from different parts of the world.

1. Gerbil from East Africa (From Buxton, 1923)
2. Jerboa from Egypt (From Buxton, 1923)
3. Kangaroo mouse, *Notomys*, from Australia (From le Souef & Burrell, 1926)
4. Kangaroo rat, *Dipodomys* from North America (From Scientific Monthly, **69**: 180, 1949.)

The third question was: Do the animals have a water storage that is gradually spent during low water intake? To determine this the water content was determined in animals that had lived on dry barley diet for varying periods of time. From Fig. 2 it is seen that the animals that had lived without water for 52 days had the same average body water percentage as the animals that had been kept without water for 14 days only. There was no difference in percentage of body water between groups of Heteromyids (kangaroo rats and pocket mice) on dry diet (barley alone) or wet diet (barley and watermelon) while white rats and *Neotoma* (wood rat, family Cricetidae) had lower percentage of body water on dry diet than on wet diet.

Since the kangaroo rats maintained on dry barley without water (1) show no weight loss, (2) excrete all of their metabolic waste products and, (3) do not get a decreased percentage of body water, we can conclude that the animals simply

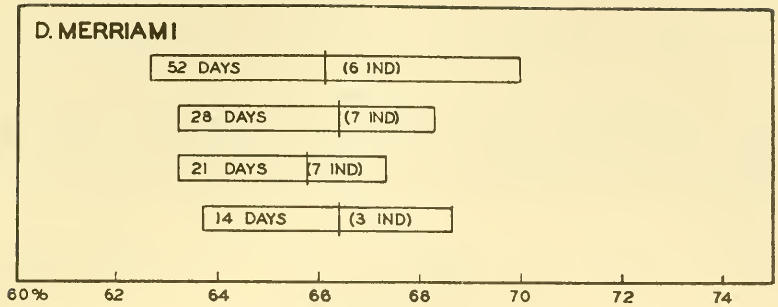

Figure 2.

Percentage of water in the body of kangaroo rats which had lived on dry diet for different periods of time. The two ends of each block represent respectively the highest and the lowest value found for the group in question. The mean value is marked with a vertical line across the block.

maintain water balance, which means that the intake of water on the dry diet is sufficient to cover their needs for excretion. They can therefore be expected to be able to live for any length of time on the dry diet.

If we want to make an account for the water intake and water output of an animal we have:

Intake	*Output*
Drinking water	Evaporation $\begin{cases}\text{skin}\\\text{lungs}\end{cases}$
Water in food	Water in urine
Oxidation water	Water in faeces

Intake

Drinking water: For the kangaroo rat the drinking water can be disregarded. No drinking water is available in their natural habitat except on rare occasions after a heavy rain fall. Dew does not occur normally, often the relative humidity only reaches about 40% at night. When kept in captivity on the experimental diet of dry barley, no drinking water was given.

Water in food: The content of free water in the food, also called preformed water (to distinguish it from the water formed by oxidation) is quite low when the diet consists of dry barley. Grain is hygroscopic and its water content will therefore vary with the relative humidity of the surrounding air. Determinations of the percentage of water in barley at different humidities gave the results in Table 1.

By storing seeds and other plant material in the more humid burrow, the animal can increase its water content somewhat. The kangaroo rats have large storages of food in their burrows.

Oxidation water: In all animals water is formed by the oxidative metabolism. The amount of water formed when a certain amount of any foodstuff is combusted can easily be computed when we know the composition of the foodstuff. Table 2 shows

that 13.4 g of water is formed when 100 kcal of barley (corresponding to 25 g of dry barley) is metabolized. This amount far exceeds the amount of preformed water at all humidities and is therefore the main intake of water for the animals living on dry grain. It cannot be increased in any mysterious way by desert animals as it has sometimes been suggested. The desert rodents can, however, economize with their water to a considerably higher degree than other mammals, as shall be shown in the following.

TABLE 1

PREFORMED WATER

Water absorbed in pearled barley (100 kcal) at various humidities

	10% r.h.	33% r.h.	43% r.h.	76% r.h.
Gram of water per 100 kcal of pearled barley (25 g dry barley)	0.93	2.55	2.93	4.53

TABLE 2

OXIDATION WATER FORMED AND OXYGEN REQUIRED WHEN PEARLED BARLEY IS METABOLIZED

	Carbohydrate	Fat	Protein	Total
Gram of pure foodstuff per 100 kcal of pearled barley	22.00	0.28	2.31	
Gram of water formed per gram of foodstuff combusted	0.56	1.07	0.40	
Gram of water formed per 100 kcal of pearled barley	12.20	0.30	0.92	13.4
Litre of oxygen used per gram of foodstuff combusted	0.80	2.01	0.95	
Litre of oxygen used per 100 kcal of pearled barley	17.60	0.57	2.19	20.4

Output

Evaporation: The evaporation from the respiratory tract is proportional to the ventilation which again is proportional to the oxygen uptake. In man the exhaled air is saturated with water vapour at a temperature of about 33°C which is slightly below the rectal temperature. When completely dry air is inspired all the moisture that is necessary to bring this air to saturation at 33°C must evaporate from the respiratory

tract. If we calculate the amount of water evaporated from the lungs of man in dry air we arrive at 0.84 ml of water per ml of oxygen utilized. In kangaroo rats and some other small rodents we measured the total evaporation (body surface and respiratory tract combined) in dry air, simultaneously with the oxygen uptake. The results are listed in Table 3. The total evaporation in the kangaroo rats per ml oxygen taken up is very low compared with the evaporation from the lungs alone in man. In the white rat the total evaporation is approximately the same as from the lungs of man.

TABLE 3

	mg. H_2O/ml. O_2 consumed
Dipodomys merriami	0.54 ± 0.01
Dipodomys spectabilis	0.57 ± 0.03
Perognathus baileyi	0.50 ± 0.03
Rattus norvegicus, var. Alb., Albino rat	0.94 ± 0.03
Mus musculus, var. alb., Albino mouse	0.85 ± 0.03
Mus musculus, House mouse	0.59
Peromyscus crinitus, Canyon mouse	0.54
Cricetus aureus, Hamster	0.59 ± 0.02

The explanation for the low evaporation in the kangaroo rats is that the expired air is saturated with moisture at the temperature of the nose which is about 10°C lower than that of the body. The white rats also have a low nose temperature and low evaporation from the lungs. The higher total evaporation from the white rats can probably be accounted for by a higher transpiration from other parts of the body. The evaporation from the skin is negligible for the kangaroo rats. The evaporation from the lungs decreases with increasing amount of water vapour in the inspired air.

We measured the relative humidity and temperature in the burrows of the kangaroo rats in order to determine how much water the animals would save by staying in their underground burrow. The measurements were done by tying small microclimate recorders to the tails of kangaroo rats and releasing the animals in front of their own burrows. The animal would carry the instrument to its nest chamber. The instrument could then be dug out after the humidity and temperature had been recorded for 10 - 12 hours.

The measurements showed that the absolute humidity in the burrows is about 3 to 4 times as high as the simultaneous humidity outside the burrow, which means a considerable reduction in the amount of water evaporated from the respiratory tract. The temperature in the burrow is much more constant than outside and always stays

below 30°C. The animal then by its nocturnal habits avoids the extreme heat of the day and can therefore avoid spending water for heat regulation.

Urine: Water can be saved by increasing the concentration of the solids in the urine. This is done to a high degree by the kangaroo rats. Table 4 shows the maximum urine concentrations in man, white rat and kangaroo rats. The kangaroo rat can excrete a much more concentrated urine than can man and the white rat.

TABLE 4

MAXIMUM CONCENTRATIONS OF ELECTROLYTES AND UREA IN URINE

	Electrolytes	Urea
Man	0.37 N (2.2%)	1.0 M (6%)
Norway rat	0.60 N (3.5%)	2.5 M (15%)
Kangaroo rat	1.2 N (7%)	3.8 M (23%)

With respect to electrolytes a kangaroo rat can excrete a urine that is twice as concentrated as sea water. This brought up the old question whether sea water can be utilized as drinking water by mammals. To test this kangaroo rats were fed on a diet of soy beans. On this high protein diet, the animals cannot maintain water balance without additional water. They were offered sea water to drink. A control group was given soy beans and tap water. From Fig. 3 it is seen that both groups of animals lost weight initially until they learned to drink, then they increased in body weight until they reached a steady state. The animals on sea water were doing just as well as the animals on fresh water. Sea water can then be utilized as drinking water by the kangaroo rat.

Faeces: The faeces excreted by the kangaroo rat are very dry compared with the faeces of the white rat. Determinations of the moisture content in the faeces of kangaroo rats and white rats and determinations of the amount of faeces eliminated when a certain amount of food was metabolized showed that the kangaroo rat looses only 0.76 g of water in the faeces when 100 kcal of barley is metabolized while the white rat looses 3.4 g of water when the same amount of food is metabolized.

Complete account for intake and output of water

With the information obtained above it is now possible to calculate at what humidities in the surrounding air the kangaroo rat is able to maintain water balance. Fig. 4 shows the result of the calculation. The calculation is based on the intake and metabolism of 100 kcal of barley, corresponding to 25 g of dry pearled barley. The ordinate gives the water intake and the minimum water output in grams per 100 kcal of pearled barley metabolized. The abscissa gives the humidity in the environmental air.

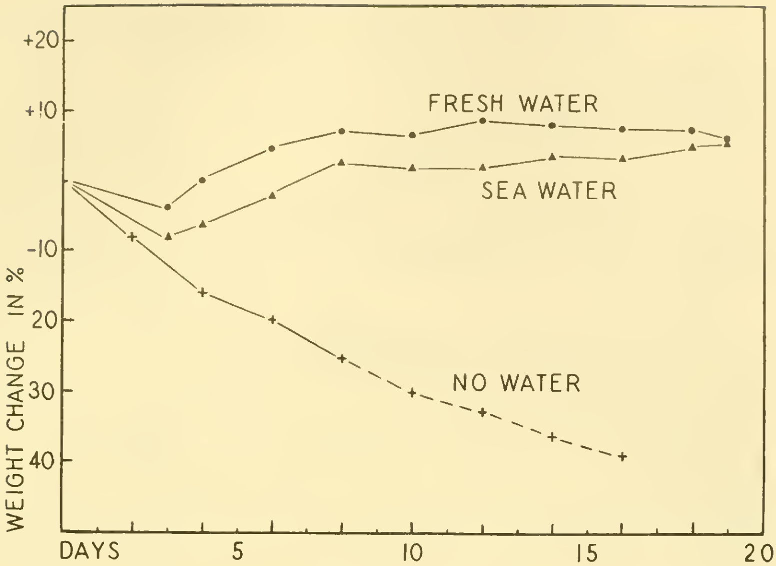

Figure 3.

Weight changes in adult kangaroo rats kept for 19 days on a diet of soy beans, given fresh water, sea water, or no water for drinking. The weight changes are given in percentage of the initial weight.

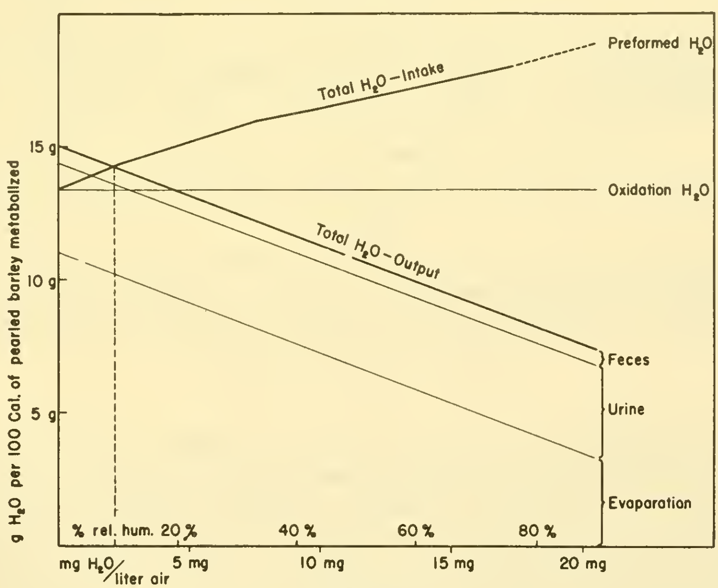

Figure 4.

Kangaroo rats; Total water intake and total water output at various atmospheric humidities at 25°C.

Ordinate: Water intake and output in grams per 100 kilocalories of pearled barley metabolized.

Abscissa: Humidity in the environmental air.

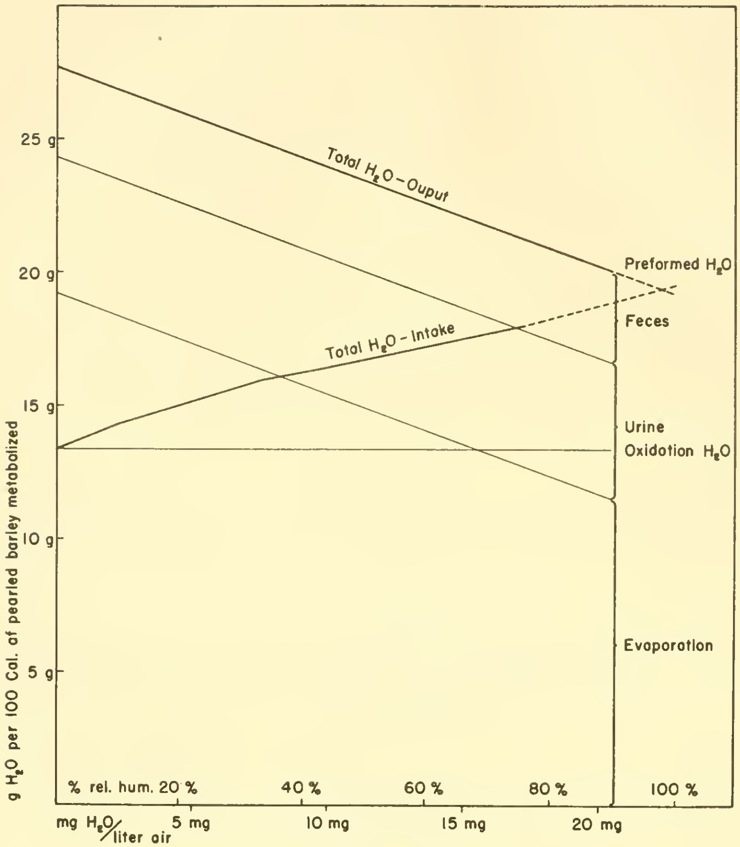

Figure 5.

White rats; Total water intake and total water output at various atmospheric humidities at 25°C.

Ordinate: Water intake and output in grams per 100 kilocalories of pearled barley metabolized. Abscissa: Humidity in the environmental air. The point of intersection for the two curves should not be taken too seriously in this graph because of inaccuracies in determining the evaporation at higher humidities.

The lowest curve shows the evaporation from the animal. The evaporation at zero humidity is calculated on basis of the determination of evaporation in dry air. From Table 2 it is seen that 20.4 ml of oxygen is used per 100 kcal of barley. Then the evaporation must be 11.0 g H_2O. The evaporation decreases with increasing water vapour content in the inspired air as shown by the sloping curve. The minimum water loss through the urine is superimposed on the curve for evaporation. It is calculated in the following way: Pearled barley contains 2.31 g protein per 100 kcal, which, when metabolized gives 0.79 g urea. The maximum concentration of urea that kangaroo rats can excrete is somewhat above 20%. The minimum amount of water required for the renal excretion of 0.79 g urea is therefore 3.4 g. The water

loss through faeces, 0.76 g is again superimposed on the two curves giving the minimum total water output when 100 kcal of barley are metabolized.

For water intake we have the oxidation water which, of course, is independent of the environmental humidity. The amount of preformed water in the barley increases with increasing humidity. The top curve gives the total water intake when 100 kcal of barley are metabolized.

From the diagram it can be seen that the water intake exceeds the minimum water output at all humidities above 2.2 mg H_2O per litre air or 10% relative humidity at 25°C. Below this value the water output exceeds the water intake, and the animals are in negative water balance.

Fig. 5 shows a similar diagram for white rats. It is seen that white rats have a considerably higher water output and cannot be in positive water balance at any humidities when they do not get drinking water with the barley.

The results in the diagrams were obtained by calculation. It was desirable to check them by actual determinations of the animals' response to changes in the environmental humidity. A group of kangaroo rats was kept at different controlled humidities at 25°C on a barley diet for periods around 10 days. The results showed that the animals can maintain or gain body weight at humidities above 10% relative humidity. At 10% relative humidity and lower the animals lose body weight. White rats were unable to maintain body weight even at 90% relative humidity when not given additional water.

In its natural habitat with its relatively humid burrow the kangaroo rat will have a certain margin of safety. The absolute humidities which are measured in their burrows vary between 7 and 14 mg of water per litre air. The humidity outside is considerably lower also at night. By its remarkable ability to conserve water the kangaroo rat shows a high degree of adaptation to its arid habitat.

HEAT REGULATION IN SMALL AND LARGE DESERT MAMMALS

Professor Knut Schmidt-Nielsen

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Desert rodents usually lead a nocturnal life and spend the day in underground burrows. In this way they escape the excessive heat load that would be imposed by high solar radiation, high air temperature and high ground surface temperatures.

The burrow temperature normally does not exceed 31°C, even on the hottest day, as shown for example by Vorhies' investigations of the microclimate of kangaroo rat burrows.

Kangaroo rats, like other rodents have no regular sweat glands and do not sweat. However, if they are exposed to high temperatures, it will be found that to some extent these animals are able to keep the body temperature below that of the environment by the evaporation of water.

In laboratory experiments it was found that the body temperature of the kangaroo rat will increase beyond the usual of 36-37°C if the surrounding temperature rose above about 35°C. A further increase in ambient temperature would lead to a corresponding increase in body temperature, apparently without causing any physiological reaction that would keep the body temperature from rising. However, if the body temperature approached the lethal limit (around 42°C) a copious secretion of saliva would occur, wetting the fur under the chin and throat, and evaporation would keep the body temperature from rising further. This 'emergency heat regulation', which is used only when conditions are critical to survival, will enable the animal to keep its body temperature even slightly below that of the surroundings for a short time.

There were differences in the reaction of different individuals, and it was found that some kangaroo rats could survive at 43°C for at least 20 minutes in experiments where white rats died at 39°C. The amount of water used for this evaporation is so great that to continue for a long time would be impossible. The animals under the conditions mentioned above had lost about 15% of their total body water, which we know is not far from the 20% which is considered the limit for desiccation that can be tolerated by mammals.

(Similar reactions of excessive salivation under heat stress have been found in other animals, such as mouse, white rat, guinea pig, cat, swine, etc. For comparison, white rats were tested in the same experiments as kangaroo rats. It was found that there was no apparent ability to lower the body temperature in the rats, and they died at much lower air temperatures (39°C) than the kangaroo rats although the lethal body temperature is nearly the same in the two species.)

The very high rates of evaporation in a small animal which uses water for heat regulation is due to the fact that the relative surface area is greater in a small body than in a larger one.

The amount of heat that should be dissipated in order to keep the body temperature constant in a hot environment equals the sum of the heat of metabolism and the

TABLE 2

The evaporation in different animals calculated from the assumption that the water loss necessary to keep the body temperature constant under desert conditions is 0.6kg. per m² body surface per hour. This value was observed in animals of 16-96kg. body weight (see Table 1). The surface areas as used in Table 2 are calculated from the formula $S = 0.1 \times B^{0.67}$, where S is body surface in square meter and B is body weight in kilogram. This is an approximation only, but of sufficient accuracy for the considerations involved.

	Body weight, kg	Surface m²	Total evaporation, kg. per hr.	Evaporation % of body weight per hr.
Camel	500	6.43	3.86	0.77
Donkey	95	2.11	1.27	1.33
Man	70	1.72	1.03	1.47
Dog	16	0.64	0.384	2.38
Jack-rabbit	2	0.159	0.0954	4.77
Kangaroo rat	0.1	0.0214	0.0128	12.8
Mouse	0.021	0.00753	0.00452	21.5

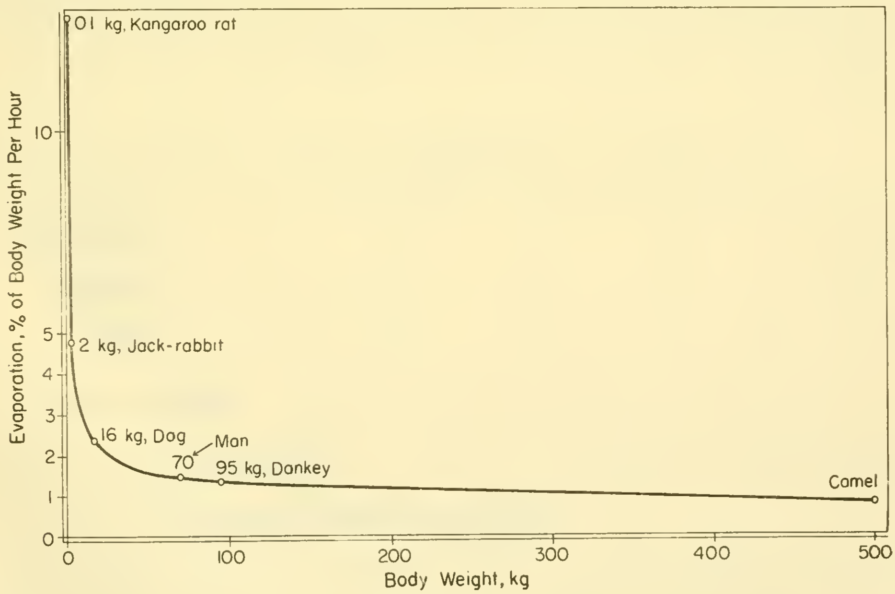

Figure 1.

The curve shows the rapid increase in evaporation of mammals with diminishing body size. The curve is based on the estimated hourly evaporation of mammals of different body size under desert conditions as given in the last column of Table 1.

heat gained from the surroundings by conduction and radiation. The heat gain from the surroundings of a physical body is proportional to the effective surface area. Also the metabolic heat of mammals is approximately proportional to the body surface, and consequently the total heat to be dissipated is roughly proportional to the surface area.

Table 1 gives a summary of rates of evaporation found under actual desert conditions in a few mammals of different body sizes. It will be seen that the dog loses body water at a rate which is more than twice as high as that of the donkey if calculated on the basis of body weight. However, we have just found that the total heat gain should be approximately proportional to the surface area of an animal, and in the table we note that the water loss per surface area actually is nearly the same in these animals, irrespective of their body size.

It would be permissible to extend this reasoning to animals of even smaller or larger body size in order to estimate how much water should be evaporated in order to keep the body temperature constant in a desert climate similar to that actually experienced in the observations given in Table 1. Such calculations are, of course, very rough approximations, and give only an order of magnitude of the expected rates of evaporation.

TABLE 1

The evaporation from donkey, man, and dog as observed in the daytime under actual desert conditions in the South-western United States by different investigators. (Dill, *Amer. J. Physiol.* **19**: 123, p. 377; Adolph, *Ibid.*, p. 371; Dill, *Ibid.*, **104**, p. 36).

	Body weight, kg.	Evaporation, % of body weight per hr.	Evaporation, kg per m^2 per hr.
Donkey (Dill)	96	1.24	0.573
Man (Adolph)	79	1.41	0.60
Dog (Dill)	16	2.62	0.657

The results of such calculations are given in Table 2. In the last column it will be seen that an increase in body size from the donkey to the camel causes a reduction in the rate of evaporation to not quite half the value. On the other hand, in small animals the rate of evaporation will increase rapidly with diminishing size. Since the relationship is an exponential function, the rate of increase gives a logarithmic curve as shown in Fig. 1. A mouse attempting to maintain constant body temperature in the hot desert would have to use water in an amount exceeding 20% of its body weight per hour. This amount of water loss is fatal, and here we find the explanation for the fact that mammals of small body size usually do not sweat or in other ways use water for heat regulation. If exposed to the heat for any length of time there would be a choice of evaporation and death from dehydration, or no eva-

poration and death from heat. The desert rodents avoid this dilemma by leading a nocturnal life and staying underground during the daytime. Only under exceptional circumstances if the body temperature should rise close to a fatal level, will they use water for heat regulation. Under these circumstances the water will last for a short time only. The actual time of survival found in the experimental work described earlier in this paper was close to that which can be calculated from the surface-body weight relationship.

It is evident that the heat exchange between the environment and the body is not as simple as assumed above. A very important factor is that the amount of heat that reaches the body from the environment depends upon the surface insulation of the body. In other words, the fur of an animal (or clothes in man) will cut down the heat gain to an extent corresponding to its insulation value. This may seem paradoxical, but it is nevertheless true that clothing in the desert reduces the heat load and therefore is of advantage to the water economy. The value of clothing in man has been clearly demonstrated under actual desert conditions by Molnar (Fig. 2). However, water economy and greatest feeling of comfort do not necessarily coincide.

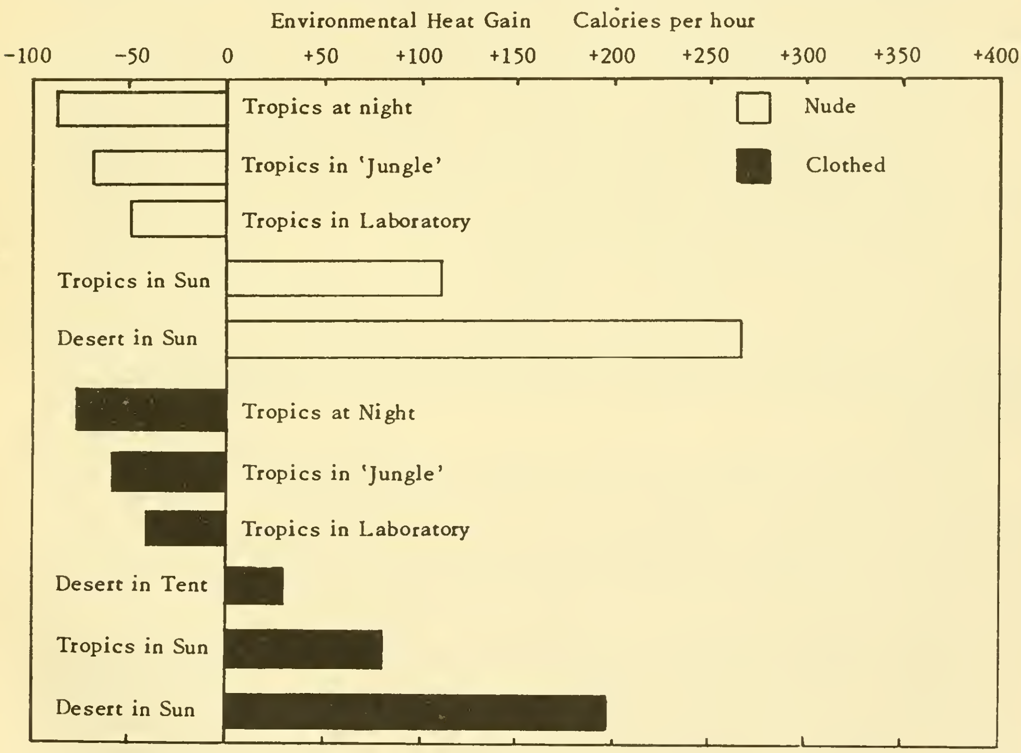

Figure 2.

This graph shows that the heat gain from a "hot" environment is much higher in the "nude" man than in the "clothed" man. The graph is taken from Molnar et al (*Amer. J. Hyg.* 44, p.417). The "nude" men wore shoes and light shorts, the "clothed" men wore light clothing including shirts and trousers. The difference between "nude" and "clothed" is particularly significant in the desert sunshine.

It has been seen that even light clothing in man cuts down evaporation by a major fraction of the total. The reduction in evaporation corresponds to the reduced heat gain from the environment, because we can assume that the metabolic heat was the same. The insulation value of animal fur is considerably higher than that of 'light clothing', and one can expect a considerable advantage in heat and water economy due to the insulation of fur.

The advantage of increased surface insulation is of course limited. It is true that an infinite insulation of the surface would reduce the heat gain from the environment to zero. This is of course not biologically possible, and furthermore, there should remain means for dissipating the metabolic heat.

The only means of dissipating heat in an environment warmer than the body surface is by evaporation of water. The heat is bound at the site of evaporation, and here we will find some relations of importance to the effectiveness of evaporative cooling.

A diagram of the animal surface is sketched in Figure 3. Water will appear in the form of sweat on the surface of the skin. It will be seen that the water either could wet down the fur and evaporate from the outer surface of the fur layer, or it could evaporate at the skin surface and diffuse as water vapour through the fur to the surrounding air. Since heat is bound at the location where water changes from the liquid state to vapour, there is a considerable advantage if the sweat evaporates at the skin surface without wetting the fur. The heat of evaporation will be taken from the body as well as the outside air, and the amounts would be in reverse proportion to the insulation of the layers between the source of the heat and the site of evaporation. The fur layer between the site of evaporation and the hot environment is a great advantage in reducing the amount of heat that reaches the site of evaporation from the environment. However, if evaporation took place at the surface of the fur, the fur layer would be a disadvantage by reducing the transport of heat from the body and it would provide no insulation between the site of evaporation and the hot environment.

It will now be clear that the most economical use of water for heat dissipation includes the fur, and an increase in the insulation is advantageous as long as it does not interfere with the dissipation of the water vapour. Furthermore, the economy in the use of water will depend upon the ease with which heat is transported from the body to the skin surface, i.e., the circulation in the skin and the insulation value of subcutaneous tissues. An increase in the subcutaneous adipose tissue would by its insulation properties directly disfavour an advantageous distribution of the heat flow to the site of sweat evaporation. It can perhaps be assumed that there would be reason to consider the distribution of adipose tissue in desert mammals from this viewpoint. The thin skin and particularly the localization of depot fat in e.g. the hump of the camel and the brahma cattle and the tail of the fat-tail sheep may indicate the possibility that this distribution may have a value in the heat and water economy as outlined above.

The principles outlined in this paper are an attempt to make it clear that active heat regulation in desert animals of small body size is a nearly impossible propo-

sition because of the large quantities of water that would be required for evaporation. They avoid the heat problems by underground life and nocturnal habits. On the other hand, the larger animals cannot lead an underground life, but due to their large size the problem of heat regulation is less severe. In the absence of exact knowledge based on experimental work, a working hypothesis can be based on a simple statement of the physical laws that govern heat exchange between the animal body and its surroundings.

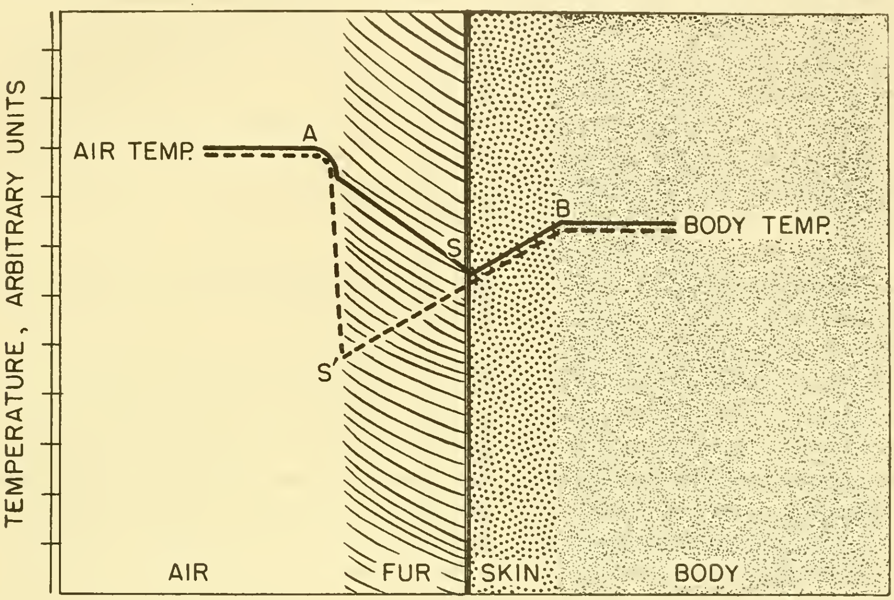

Figure 3.

A simplified diagram of the temperature gradients at the surface of an animal when the ambient temperature is higher than the body temperature. The temperature gradients indicated by the solid line ASB and the broken line AS' B, respectively, show in which direction heat flow will occur under different circumstances. If sweat evaporates at the surface of the skin (S) without wetting the fur the temperature gradients will be as given by the solid line ASB. If sweat evaporates from the surface of the fur (S') the gradients will be as shown by the broken line AS' B. In both cases heat flow to the site of evaporation from each side, but it is evident that much less water is required to maintain the gradients indicated by ASB than by AS' B. In order to maintain constant body temperature the total heat flow along the gradient BS must equal the metabolic heat. In the case of evaporation from the surface of the fur, this gradient would have to be extended to S', requiring a lower temperature at S' than at S. This lower temperature would further increase the steepness of the gradient AS', which governs the heat flow from the air to the site of evaporation. The heat flow along the less steep gradient AS (when water is evaporated at the skin surface) is much lower, and the steepness (and the heat flow) will decrease as the insulation value of the fur layer increases. It is further evident that a reduction of the insulating value of the skin itself (reduction of the distance BS) will permit a steeper gradient to be set up for the heat flow from the body to the surface, without a simultaneous increase in the steepness of the gradient AS. In other words, the heat flow from the body to the surface is facilitated by a thin skin of low insulation value.

REACTIONS TO GREAT ENVIRONMENTAL HEAT IN ANIMALS

Dr Frank Marsh
(*London*)

The sun, we are told, is a shining example of an atom bomb. It is difficult for people living in England – where the sun is rarely seen, and the weather is a national joke – to have any idea of the severe trials undergone by travellers or indigenes in the Arabian Desert, or even in the cooler Sahara. The celebrated Western Desert between Tripoli and Alexandria is probably cooler still; but this statement may be disputed. 'Animal Life in Deserts' is a big subject treated scientifically in the classical publication of that name. The modern problem is to provide living space for an ever increasing human world population, and also to provide adequate nutriments for this human mass. The great deserts of the world, the Sahara, the Arabian deserts, the Central Asian deserts, the deserts of California and Mexico, the Australian deserts and the cold deserts at the poles are all being thoughtfully surveyed by contemporary man. These great sterile wastes can all be made fertile, green and productive by capital expenditure – as shown by Ritchie Calder in 'Men Against the Desert' – and by the Tennessee Valley Authority in the United States of America. Geologists and technicians know that 'wild cat' expenditure of capital may provide very substantial returns for a relatively small outlay. Valuable minerals and oil are nearly always found in barren, rocky or sandy wastes, far from the outposts of civilization and subject to all climatic extremes, The fact that some very valuable raw material is found even in the middle of the Sahara, causes an immigration of technicians and their associated civil engineers, surveyors, domestic and administrative staff and other parasites, who may include even a rude medical or health service. This closely knit community will develop gardens, bushes, shrubs and small trees, to mitigate the severity of the landscape, filter the hot winds, provide some fresh vegetables and add to the amenities of clubs and dwellings, however rudimentary. A little oasis will appear in a situation that – a few years earlier – was nothing but a howling wilderness. This miraculous transformation – for it is nothing less – is due to the patient spare time efforts of men, and their devoted wives, with a desire for the amenities of life, but with no special knowledge of desert reclamation, except what could be picked up as they went along. The men who construct these commercial installations 'in the blue' are mercifully free from many of the disorders of civilization; they do, however, risk a number of unfamiliar disorders which are not absolutely confined to the brown tropics, but can be described as very rare in temperate regions. One of the most dramatic and disabling of these exotic afflictions of men is the syndrome often referred to as 'effects of heat'. The effects of heat are, shortly, dehydration, high fever, affections of the skin, with unconsciousness in the acute or hyperthermic cases, and lassitude, debility, faintness, malaise, slight fever, cramps, tetany, headaches, weakness and other symptoms in the prodromal, sub-acute or chronic varieties of the disorder. Effects of heat are preventable, and should be prevented in any settled community, but the 'wild cat' pioneers have none of the resources of civilization and take great risks. Observations on the effects of heat on utterly unprotected personnel impelled me to

make a study of these acute manifestations in the hope of devising a rational, and if possible, effective form of therapy. The mortality rate in human victims of hyperthermia or heat stroke is very high; effective therapy is an acute necessity: in War perhaps even more than in Peace.

Our experimental animals were rabbits; they cannot sweat; the rabbit attempts to cool its body – in a hot environment – by breathing quickly over the moist red tongue and lips. In our initial experiments the emphasis was on respiration; after exposure to the sun (138°F) the rectal temperature of an adult healthy rabbit reached 110.0°F with respiration rate 125 per minute, carbon dioxide exhaled 230 ml/sq.m./min. and volume of expired air 2100 ml/min. *Ice* was then applied to the whole of the fur and the rectal temperature dropped to 104.0°F, the respirations, carbon dioxide and volume falling to 120, 190, and 1700, but rising again to 140, 250, and 2700 at the end of the experiment. The animal made a complete recovery but gave birth to two stillborn young a few hours later. As a result of a number of experiments we found that if the respiratory activities were *stimulated* by a rising body temperature, the animal tended to recover. At the peak of body temperature some animals collapsed; one such with a rectal temperature of 112.2°F stopped breathing: the carbon dioxide in the exhalations had increased as the body temperature rose, but there was no compensatory increase in ventilation; the respiratory centre in the brain appeared to have become relatively insensitive to increases in the carbon dioxide tension in the blood. Cyanosis was not observed in this animal, so the brain cells may have been depressed by some other factor, mere heat or reduction of the blood pH. This collapsed animal responded to ice applied to its fur, and behaved normally for some hours, after its body temperature had been reduced, but late in the evening he was discovered with a subnormal rectal temperature, pale ears, inaudible heart beats, sighing respirations and very weak. The respirations had dropped to 60 per minute. This animal was painlessly destroyed to avoid further suffering and portions of the body tissues were preserved for histological examination.

Another rabbit showed respiratory stimulation in the early stages of the experiment, with respiratory depression near the peak of the body temperature (108.0°F) but the respirations quickened again after cooling treatment. The ventilation increased in response to the increased concentration of carbon dioxide in the exhalations – and presumably, increased carbon dioxide tension in the blood – an indication that the respiratory centre in the brain was sensitive and reacting normally; a good sign. Yet another rabbit suffered a rise in rectal temperature to 113.6°F rather quickly and died suddenly at the peak; before the crisis he had responded well. Still another rabbit was taken up to a peak temperature (rectal) of 111.1°F respiratory stimulation was shown until the crisis was reached, when there was a short period of depression, followed by further stimulation on cooling. This rabbit appeared to have been successfully treated, and made a good recovery, which, however, proved only temporary. Having spent the night in comfortable cool surroundings, he was found dead next morning.

Provided the rectal temperature did not exceed lethal levels, the cardio-vascular system seemed to adjust itself to the high body temperature during the acute phases of heating up and cooling down. If the cooling process was delayed or omit-

ted, there were profound effects. But in some cases the acute phase was successfully negotiated and complete recovery seemed in sight, when a crisis of depression occurred, of obscure origin and usually fatal. (This sequence of events is not unfamiliar in human cases of hyperthermia).

A very successful type of rabbit was a black female – No. 60 – exposed entirely in the shade. Rectal temperatures were:- initial, 104.1°F rising to 112.7°F and then, with cooling, falling to 101.0°F. Haemoglobin had an initial value of 105% gradually falling to 92% at which level it remained for 28 minutes, then rose to 105% at the rectal temperature peak and to 113% at the conclusion of cooling treatment. Blood pressure was not estimated. Carbon dioxide and air volumes exhaled were according to expectations. The heart beats of this rabbit were counted with a binaural stethoscope (by tapping on a sheet of paper for ten seconds) on twelve occasions during the experiment. Initially the heart beats were 288 per minute and loud, increasing gradually with increase of body temperature to 350 beats per minute, loud, continuing loud and rapid until just after the rectal temperature peak, when the beats were 350 per minute and quiet. After cooling the beats were 300 per minute and loud again. This rabbit recovered without complications.

Rabbit No 73 had a similar shade treatment, but is chosen because of the record of blood pressure. Initially rectal temperature was 104.2°F and blood pressure was 64.0 mm.Hg. rising to 80.0 mm.Hg. at rectal temperature 109.0°F and falling to 42.0 mm.Hg. at the rectal peak of temperature (111.0°F). In the early stages of cooling the blood pressure rose abruptly to 120.0 mm.Hg. and then fell, equally suddenly, to 20.0 mm.Hg. with recovery to 80.0 mm.Hg. about ten minutes after the cessation of the cooling treatment. This rabbit also recovered completely, without complications.

Several rabbits developed cyanosis, apnoea, and almost inaudible heart beats at the apex of rectal temperature, i.e. between 111.0°F and 114.0°F. In one case, the rabbit became cyanosed, stopped breathing, and was treated by ice pack, without avail. In this animal some three minutes after apparent death (cessation of respiration with unconsciousness) the heart was still beating at 80 beats per minute.

One rabbit of this group showed a blood pressure fall from 70.0 mm.Hg. initially, to 40.0 mm.Hg. at rectal temperature 105.6°F then, at rectal temperature 107.8°F recovered to 70.0 mm.Hg. and at rectal temperature 109.8°F was still 60.0 mm.Hg. Then the blood pressure fell suddenly to 36.0 mm.Hg., made a jerky recovery to 65.0 mm.Hg. at the rectal temperature peak (112.0°F) and fell to 10.0 mm.Hg. in less than five minutes. Ice pack treatment was unavailing, death occurred in a few minutes. With sudden death at the peak of rectal temperature all the body systems, respiratory, circulatory and nervous, seemed to be simultaneously depressed, probably from the effects of heat on the nerve cells of the brain, including the respiratory and other centres, and on the regulatory centre in the hypothalamus. This problem of brain lesions will be approached later.

For the problem of delayed death some details of rabbit No. 22 will be considered. This female albino rabbit was restless and struggled throughout the exposure, entirely in the shade. Initially haemoglobin was 95.0% at rectal temperature 104.2°F when the blood pressure was 75.0 mm.Hg. The haemoglobin rose to 114% at

the rectal temperature peak (112.0°F) but the blood pressure fluctuated jerkily from 66.0 mm.Hg. to 90.0 mm.Hg. then from 76.0 mm.Hg. to 90.0 mm.Hg. at body temperature 111.2°F followed by a rapid fall to 34.0 mm.Hg. and with recovery to 66.0 mm. Hg. at the conclusion of the cooling treatment. This rabbit responded to a rising body temperature by increase of respiratory activities, ventilation being adequate for the carbon dioxide levels in expirations until the body temperature 111.8°F was attained. At this point there was respiratory failure, characterized by unresponsiveness of the respiratory centre at the body temperature peak and progressive deterioration during the cooling treatment, there being no sign of stimulatory response for the respiration during this phase. The blood pressure, however, responded favourably, at the conclusion of cooling treatment.

It may be significant that the circulation appeared to be favourably influenced by cooling treatment to which the respiration was unresponsive. There was no apparent addition of fluid to the intra-vascular system during the phase of heating up; and there appeared to be progressive loss of fluid from the circulation after the body temperature 107.8°F continuing steadily up to the peak of body temperature; haemoglobin rise 19%. At the conclusion of the acute experiment, the rabbit was rather dazed, but otherwise seemed in good condition. Examined at 9.30 p.m. that day she was found lying on her side, unable to stand or walk, breathing rapidly, heart rate 240 beats per minute, sounds quiet but audible. The rectal temperature was 88.6°F (subnormal) the room temperature at this time was 96.8°F. The blood pressure was too low to record. While we were attempting to obtain blood for a haemoglobin estimation, the rabbit gave a number of violent inco-ordinate movements and died at 9.40 p.m. At autopsy, performed immediately, the limbs and abdominal muscles were very stiff, heart contracted and hard, petechial haemorrhages in the walls of the small intestine, bladder distended with brownish fluid, ears very white, suprarenals very pale in colour, abdominal viscera deeply engorged, fluid in the peritoneal cavity under pressure, limb muscle white. The death of this rabbit appeared to be due to some form of peripheral circulatory failure, emphasis being probably on capillary damage rather than failure of the heart or vasomotor centres, except perhaps as a secondary effect. The associated poikilothermia, however, may have been due to damage to the controlling centres, since the respiratory centre became unresponsive after the exposure, and showed no sign of improvement during cooling; even though the blood supply to the respiratory centre – judging from the recorded blood pressure – should have been adequate, in the absence of spasm of the cerebral arteries and arterioles. (This suggestion is at variance with physiological dogma, but we have several instances where the only explanation for central failure seemed to be spasm of the cerebral arteries or arterioles.)

Our time is getting short, and I have outlined some of the problems involved in the effective treatment of cases of heat stroke. Rapid cooling of the whole body was the best treatment for the hyperthermic crisis; the delayed collapse in cases successfully cooled was combated in a number of ways; very useful was an extract of the cortex of the suprarenal gland, injected subcutaneously. The associated damage to the central nervous system was investigated; we found focal ischaemic areas scattered throughout the cerebral hemispheres, the cerebellum, and in some

cases the hypothalamus in autopsy material. Over thirty normal rabbits, submitted to multiple episodes of sub-lethal hyperthermia and then autopsied and serial sections cut of every brain showed no such lesions. Focal areas in the brains of men killed by hyperthermia have been found by American observers; but the American material was always haemorrhagic, in contrast to our findings which indicated ischaemia. The Americans gave narcotic to their human cases before exposure to great heat. Clinical signs of cerebellar damage have been reported by British observers in human cases as a sequela of hyperthermia (heat stroke) and some American observers have demonstrated destruction of the nerve cells in the hyperthermic nuclei in such cases. There is a tendency for those patients not killed at once by their brain injuries, to recover with suitable cooling therapy and supportive treatment for the circulatory depression.

Nervous sequelae may occur in these recovered persons, and sometimes the nervous changes clear up with a passage of time in a temperate climate: not all do, however. There is not time to describe any further experiments; even if the patience and enthusiasm of this exemplary audience could bear any more of this rather technical and unexciting chronicle. We have to thank Sir David Brunt for rescuing the subject of heat effects from oblivion, and for rescuing it from obscurity by clothing its scientific nakedness in mathematical expressions, which, though hardly the glass of fashion or the mould of form, none the less are graceful and elegant interpretations. I have also to thank Dr J. L. Cloudsley-Thompson for the opportunity to give expression to my views.

HUMAN ADAPTIBILITY TO HOT CONDITIONS OF DESERTS

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The ten or so major hot desert regions – Sahara, Kalahari, Thar, Persian, Turan, Gobi, Arabian, Mohave, Atacama, Argentinian – are of interest physiologically because of the combination of the following characteristics; the high air temperatures, the high intensity of solar radiation, the occurrence of fierce hot winds, the low humidity and the diurnal and seasonal fluctuations. Daytime dry bulb temperatures in the shade may greatly exceed normal body temperature, maxima as high as 135°F have been noted; mean daily maxima of 100°F and over occurring on 50 days or more in the hot season, or of 95°F (i.e. very close to body temperature) on about 100 days, are on record for the Sahara, Arabian, Colorado, Australian and Thar deserts. Such temperatures imply not only the cessation of an appreciable convective heat loss from the body but a large addition of heat to the body from the ambient surroundings; when winds prevail the convective heat load will be still further increased roughly in proportion to the square root of the impinging air speed. Some gain of heat to the body by conduction also occurs in the desert since surface temperatures of 150°F even 170°F may occur. Over and above these sources of desert heat there is the high intensity of the sun's radiation, unhindered by atmospheric moisture and added to by re-radiation from hot surfaces. The magnitude of the heat flow to the body and its capacity for dealing with it are considered below. The physiological severity of the desert depends on the intensity and duration of the daily hot spells in the summer season and it is for such short exposures that most information is available from physiological analysis. A certain amount of data has been obtained at first hand by investigations in deserts. The most notable work is that of Adolph (1947) and Dill (1938) in America and the more clinical work of Ladell (1944) and Horne & Mole (1950) in the Persian and Pakistan regions. The great bulk of our data has been obtained in studies in artificially heated rooms. Nearly all these studies give an insight into the effects of relatively short exposures but in few of these have high radiant temperatures figured very much. Far less is known about the effects of the extreme swings in temperature experienced in many desert areas or of the cumulative effects over a season or a period of years. Some insight into the nature of long-term effects is provided by a consideration of the physical characteristics of the people indigenous to the desert.

1. *Ethnology*

Probably less than one per cent of the world's population endure desert climates. Yet even this number and the variety of the peoples it represents furnishes obvious evidence of the capacity of man as a species to withstand the thermal rigours of such environments. The principal hot arid regions provide an interesting ethnological picture which can only be presented in outline here. The central Asiatic desert is part of the territory of a mixed stock whose affinities become progressively more Mongoloid as one passes across the Gobi, and increasingly Turki-Alpine in the plains west of the Pamirs. In the Thar desert there is a complex of groups difficult

to classify – the Sodas and Khoras and the nomadic Udejas and some members of the Bhils – representing on the whole elements akin to European varieties. The Middle Eastern – North African deserts contain folk of Caucasian, i.e. European affinities belonging principally to the Mediterranean variety; such are the Ruwala Bedouin and the Tuareg. There is also in this N. African desert region a fringe of Negro peoples. The Kalahari contains the Southern Bushmen, who, on blood group and other data, should be considered of Negroid affinity. In the desert strip called the Namib, Negros of the Ovambo tribe are to be found. In or near the South Western deserts of N. America there are American Indians (like the Hopi) as also in the Atacama desert. The Australian desert may be regarded as uninhabited in its main central area yet there are many tribes such as the Arunta who endure the rigours of a desert climate. A handful of Europeans in Australia also experience quite severe desert conditions.

This sketchy description shows sufficiently that, where the desert heat load has to be endured, the human species in all its varieties, Negro, Mongoloid, European, Australian, has the physiological capacity to deal with it, even allowing that many of the peoples mentioned have probably not come into desert conditions by choice and that the populations are often nomadic and in many cases only semi-permanently in these regions. The ethnological data gives strong a priori grounds for supposing that the human physiological make-up does not itself constitute a primary or major bar to the greater penetration and development of desert regions. Nevertheless, there is a considerable adjustment needed, as will be shown, for existence in these conditions, even for short periods, and a knowledge of these can contribute much to successful and more extensive human activity in these parts of the world.

2. *The Discomfort of Desert Conditions*

Stimulated by the requirements of ventilating engineers, considerable investigation has been made in Europe and America on the relation between ambient conditions and subjective impressions of warmth so that for individuals living in these countries, these can be stated with some precision (Bedford, 1948). This is usually and conveniently done in terms of the American Effective Temperature scale which enables one to specify the subjective effect of any combination of wet bulb, dry bulb and air movement (and radiation) as a single temperature. When the effective temperature exceeds 70°F, many people in temperate climates move out of the 'comfort zone' and above 75°F the majority will complain of the discomfort. Such figures refer to people lightly clothed, sedentary, in the summer; in winter, tested in the same way, these levels will be found to be too high, that is, there is an increased tolerance to heat in the summer showing the existence of an acclimatization process. It is to be expected therefore that individuals who have lived for long periods in hot climates of the world would show a similar increase in subjective tolerance. Native-born white Australians, according to the recent investigations of Drysdale (1951), can tolerate without undue discomfort an upper limit of warmth as high as 80°F effective temperature. At such temperatures the skin may be quite moist but there are few complaints on this score. Results in other hot places (Iran, Singapore, India) generally confirm these high limits though in some cases differences in clothing may have been operative in the tests.

The severe shade conditions of deserts may now be viewed in the light of these values. In the table, the desert effective temperatures are given for two levels of air speed, fairly still air (30 ft/min.) and air at 300 ft/min. (4 m.p.h.), at two levels of humidity, namely 20 and 30%, for individuals wearing light clothing.

Air speed:-		30 ft/min.			300 ft/min.		
Dry Bulb: °F		95	105	115	95	105	115
R.H. 20%	E.T. °F =	77	84	88	74	82	87
R.H. 30%	E.T. °F =	79	85	92	76	79	90

It will be seen that up to dry bulb temperatures as high as 105°F desert conditions yield effective temperatures not far from those which appear to be just tolerable for individuals acclimatized to hot climates. These figures, admittedly only approximate, do enable one to evaluate more objectively the limits of tolerance to be expected in desert conditions and in fact, despite the greatly increased heat flux the body must cope with (see below) these limits are probably higher than usually thought to be the case. No studies of indigenous people, however, appear to have been made from this as from other points of view. The nature of acclimatization is also by no means understood though, as we shall see, there are certain physiological changes in the body which proceed in parallel with increased tolerance.

3. *Capacity for Work*

As indicated in the table, the desert on many days in the summer affords conditions, even in the shade, more trying than the upper limit of the 'comfort zone' of 80 – 82°F effective temperature of acclimatized individuals. The heat load on the inactive indoor individual is derived by convection and radiation from the surroundings. Out of doors the direct and indirect solar heat load will be added to these. Nevertheless it can be shown that there yet remains a fair margin to the body's capacity to maintain homeothermy even after dealing with the heat gain from the exterior. This is the margin available for coping with the heat production of muscular work. To understand how great this margin is likely to be it is only necessary to consider the maximum rate of cooling which the body is physiologically capable of developing. In the desert conditions under consideration this is entirely dependent on evaporation of water from the skin surface (that from the lungs adding only about 5 – 10%). It is possible to predict the *maximum* cooling capacity of the body for any particular set of desert conditions where the total surface area of the skin surface is regarded as effectively wetted and where a skin temperature of not higher than say, 97 or 98°F is assumed. In fact, a physical body shaped like the human body, kept wet at this surface temperature, could lose heat at the rate of about 500 or 600 Kcals/hr up to air speeds of, say, 5 m.p.h. In very severe desert temperatures (E. T. of 90°, air movement 300 ft) the convective heat load impinging on the body might be of the order of 100 Kcals/hr, the radiation heat load on a man in the standing position might be about 150 Kcals/hr, so that 250 Kcals/hr remain for metabolism and work but this margin would drop off rapidly as the air movement fell.

This simplified account indicates that the maximum ability of the human body on physical grounds to maintain heat balance demands an output of about 1 litre/hr sweat for a cooling equivalent to 500 Kcals/hr. (It is as if the provision of sweat glands had been evolved to cope with heat loads as high as that required for life and activity in hot dry regions rather than for the lower heat loads of hot humid tropics). In actual tests on Europeans this sweat rate (1 litre/hr) is indeed about the limit of what the sweat glands can manage to maintain for 4 – 6 hours. It is not surprising that physiological acclimatization, as we shall see, improves the performance of the sweat glands and that efficient performance as well as breakdown in the desert for the most part is a matter of water supply and water metabolism as abundantly illustrated by the work of Adolph and his colleagues.

4. *Some Physiological Adjustments*

The changes which we know occur in the heat regulatory system, the circulation, the kidney and the endocrine system cannot be dealt with in any detail here. But it is important to realise that short term exposure to heat induces circulatory effects primarily to facilitate a greatly increased loss of heat from the surface, and as this depends so much on sweating, there are consequent adjustments in water (and salt balance) throughout the body. It is the regulation of these that calls for endocrine activity by the posterior pituitary and the adrenal cortex – to mention only those glands for which we have evidence.

Salt Intake Of these processes it is worth mentioning in a little more detail the great capacity possessed by the human body for adjusting its salt loss to the supply (Weiner & van Heyningen, 1952). It was first noted by Dill and his colleagues that sweat of people living in the desert became progressively reduced in its salt content. This is now known to happen only when salt intake is initially rather low. The kidney in such circumstances immediately cuts down its salt concentration and output and this is followed in a few days by a similar reduction in salt composition of sweat. The normal sweat gland is in fact able to do considerable osmotic work in producing a hypotonic fluid though this falls as high rates are approached. Many individuals can thus, after a period of adjustment, subsist in hot conditions on a moderately low salt intake. There is however evidence of great individual variation in this respect and the process may be attended by undesirable symptoms and a lowered capacity for work. Salt imbalance is probably one of the commonest causes for upset in hot conditions before acclimatization asserts itself. The evidence favours the additional consumption of salt when sweating increases and water intake is correspondingly high.

Sweating and Acclimatization Acclimatization proper to hot desert conditions shows itself in an increased capacity to perform muscular work and a concomitant improvement in bodily heat regulation, as shown by a progressive reduction in the pyrexia induced by high heat loads. There is a concomitant increase in the sensitivity to heat stimulation of the sweat glands as shown both by some increase in sweat production for a standard heat load and by a more rapid response. The acclimatized man accumulates less heat and must therefore handle a greater heat loss, or to put it another way, he purchases reduced discomfort and high efficiency by a lower

skin and body temperature and must therefore remove more heat by evaporation. The earlier and greater output by the sweat glands of acclimatized individuals has been noted in many laboratories to occur on the first 7-14 days of continuous or repeated exposure. It may be detected even after a year of living in hot climates. In desert conditions where sweat is so readily evaporated it certainly appears to be an adjustment of real importance.

It should be repeated that we have no first hand data of the indigenous desert peoples or on those who have lived long periods in desert regions.

5. *Breakdown*

Enough has been said to indicate that adjustment to severe desert conditions is physiologically of a complex nature and it is not surprising that this may fail at different points. There is also great individual variation in liability to these failures of physiological adaptation, at least in Europeans, for information on indigenous peoples is lacking. Brief consideration of these disorders will serve to indicate the nature of the physiological breakdown.

a. Circulatory failure with syncope occurs in most heat disorders but in a simple form it is often the outcome of insufficient acclimatization and training for hard work at high levels. In deserts it is often the sign of incipient dehydration or of salt imbalance.

b. Dehydration resulting from lack of water in relation to heat load is by far the most serious danger in deserts. The body's ability to deal with water shortage is more limited than its capacity to compensate for salt shortage. The number of days of survival in the desert can be readily calculated when water supply fails. This has been dealt with in a thoroughgoing manner by Adolph and his colleagues who have mapped these survival limits for all desert regions and for different conditions of work allowing for movement either at night or day. There is no evidence at all that individuals can be 'acclimatized' or 'hardened' to a low water level. Enforced reduction in water intake does not reduce the deficit of body water by sweating. Performance in the heat is better if water is taken continually. Fortitude when water is short is to a large extent a matter of morale. The work of Adolph should be consulted for a vivid account of the key importance of water supply not only to survival but to efficiency in day to day work in the desert. Adolph describes many practical ways of reducing water requirements such as the best use of shade and clothing.

c. Lack of salt may produce relatively mild effects such as undue fatiguability or severe cramp of the abdomen and limb muscles. As already indicated, there is good physiological compensation for low salt intake but it is likely that some individuals are far less efficient in their ability to conserve salt by reducing its concentration in urine and sweat. The desirability of supplementing salt has already been commented on.

d. Sweat gland fatigue can be demonstrated in laboratory studies but its exact relationship to the apparently complete cessation of sweating seen in the failure of heat regulation with hyperpyrexia, known as 'heat-stroke', is not clear. In

the condition known as 'anhidrotic heat exhaustion' there is evidence of actual damage to the sweat glands as a result in many cases of pre-existing prickly heat. It has also been claimed that injury to sweat glands is likely in the early stages of sunburn. Such damage brings about a greatly reduced capacity to carry out active work in the heat for the lack of sweating makes exertion very unpleasant and inefficient and circulatory failure is easily induced. This condition and certainly prickly heat are both far more common in hot humid climates than in desert conditions and could only occur in closed spaces with extremely poor ventilation.

6. *Desert and 'racial' selection*

It has earlier been pointed out that representative groups of all the varieties of mankind (whether these are classified serologically or morphologically) are to be found in deserts, so pointing to the adaptiveness of mankind as a whole. Indeed, laboratory tests have shown that short term acclimatization phenomena are similar in Europeans, Asians and Africans. Nevertheless, this does by no means preclude the possibility that these desert sub-groups have undergone distinctive changes as a result of continuous residence in the desert. Evidence has accumulated that in regions of high mean annual temperature some differences in bodily development and in physique are encountered. D. F. Roberts in this laboratory has shown that peoples of hot climates are of lower body weight and often in addition exhibit an elongation, relative to trunk, of either upper or lower limbs or both, as compared with people in temperate and cold climates. Probably 50% of the variance in these characteristics is attributable to differences in mean annual temperature. These modifications in physique will be recognised as being in line with Bergmann's and Allen's Rules and it could be argued on physical grounds that they represent advantageous adaptations to hot climates. However, the existing records relate overwhelmingly to peoples in the hot humid regions and it is by no means clear whether desert peoples universally exhibit these physical characters. Nor is it certain that such changes are necessarily genotypic. Another effect of hot humid climates (which may be merely phenotypic) is a slowing down of the rate of skeletal maturation and sexual maturity. Again, data for desert peoples is lacking.

The most striking of all 'racial' characters associated with desert people is of course the steatopygia of the Kalahari bushmen. While there has been some speculative discussion as to the role of this fat deposit as a fuel and water store, no direct study has yet been made. Some of the Andamanese pygmy negritoes show similar female steatopygia proving that the condition is to be found in humid tropics as well as in deserts.

Yet another problem is the significance to be allotted to melanin pigmentation of the skin and here again, owing to lack of adequate technique, no objective comparisons of skin colour amongst desert people can be quoted though one can be certain that a great range of skin colour must exist. The general opinion that melanin deposition is protective against ultra-violet light and of value in hot climates is strengthened by some recent experiments of Thomson (1951) in which he showed that in Europeans sunburn can be associated with damage to the sweat glands. Another

pointer in the same direction is the greater incidence of rodent ulcer in white Australians which is presumably attributable to some special sensitivity to solar radiation.

7. *Conclusion*

This outline should serve to show that life in deserts is well within man's physiological capacity as of his technology and organisational ability. Disorders occurring purely as a result of the climate are to a large extent preventable and a matter of fairly simple hygiene. The fact is that rules of living have to be acquired for desert life as for other parts of the world and that this can be done efficiently is obvious from the successful survival of the great variety of desert peoples. The realisation that this adaptability, as well as its limits, is being given a progressively more exact physiological analysis should serve as an encouragement to the more intensive interest in the development and amelioration of deserts.

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LE PEUPLEMENT HUMAIN DU SAHARA

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Les préhistoriens nous enseignent qu'à l'âge de la pierre un ciel pluvieux arrosait le Sahara, de l'Atlantique au Tibesti, de l'Atlas et des Syrtes au Niger et au Tchad. Une végétation abondante y nourrissait une faune tropicale, des éléphants et des hippopotames. Une population, que l'on a des raisons de croire de race noire, l'habitait. Puis, vers la fin de la période néolithique, les nuages reculèrent vers le Nord, le desséchement progressif du sol tua toute vie, créa le désert. Alors les peuplades noires ont abandonné une terre devenue aride et ont émigré vers le Sud, laissant d'innombrables témoignages de leur existence, armes et outils de pierre taillée, gravures et peintures repestres, que l'on a actuellement la surprise de découvrir épars dans des régions nues et désolées, sous un ciel de fournaise. La régression des Noirs au Sud du Tropique fut suivie plus tard de l'avancée de Berbères blancs peu nombruex, venant des rivages méditerranéens.

On estime à 3 millions le nombre d'habitants éparpillés actuellement sur les 8 millions de kilomètres carrés que couvre le Grand-Désert, entre l'Atlantique et le Tibesti, ce qui correspond à une densité démographique inférieure à la moitié de l'unité. Dans les Territoires du Sud algérien, dont la superficie est d'environ 1,981. 000 km², la population totale était, en 1948, de 817,000 âmes; la densité au kilomètre carré était donc de 0.4. Le Fezzan, dont on évalue l'étendue à 800,000 kilomètres carrés, compte 50,000 âmes; la densité démographique y est donc de 0.06 par kilomètre carré.

Montesquieu a écrit: 'Quand un pays est désert, c'est un préjugé de quelque vice particulier de la nature du climat'. Le vice du climat saharien est d'être un climat d'extrêmes. Ses trois facteurs dominants sont une aridité extraordinaire, — une grande chaleur estivale contrastant avec un froid relatif hivernal — des vents impétueux.

On peut définir comme zone aride une région qui ne possède aucun cours d'eau normal et qui reçoit rarement de la pluie (moins de 100 millimètres par an, durant une période assez longue).

La seconde caractéristique météorologique du Sahara est une température excessive et à variations brusques. Le thermomètre marque souvent, pendant de longues semaines, de mai à octobre, 50° et plus, jusqu'à 58°. Mais l'hiver est assez froid: au centre de Sahara, à des altitudes qui ne dépassent pas quelques centaines de mètres, on compte de 1 à 3 semaines de gelée par an, le minimum absolu decendant à quelques degrés au-dessous de zéro. D'autre part, le rayonnement nocturne, intense, cause des écarts qui peuvent dépasser 30° entre la chaleur accablante du jour et la fraîcheur de la nuit.

Après l'aridité et les températures extrêmes, les vents contribuent à donner au climat du Sahara son caractère de violence et de rudesse.

Les effets de climat saharien sur la nature sont d'une étrange brutalité.

L'érosion fluviale au Sahara a été très considérable aux temps préhistoriques. L'action de l'érosion éolienne, qui se poursuit de nos jours, est immense. Elle décape le sol, le dégrade.

Les ennemis des plantes au Sahara sont multiples: la rareté et l'extrême irrégularité des pluies, la sécheresse de l'air et l'absence de rosée qui en résulte, l'aridité du sol, les fortes chaleurs estivales et les froids hivernaux, l'insolation intense, la fréquence et la violence des vents. L'agriculteur ne peut faire que des cultures irriguées, des jardins, qui sont les oasis, dans les points extrêmement rares où une eau souterraine affleure le sol ou se trouve à une profondeur accessible. A l'ombre des dattiers, on cultive des arbres fruitiers, des légumes, quelques céréales.

La faune saharienne comporte de nombreux genres et espèces, mais les espèces y sont représentées par un petit nombre d'individus. Le seul élevage qui réussisse bien au Sahara est celui du chameau, qui se contente comme nourriture des plantes ligneuses et épineuses des plateaux pierreux (les hamadas) et des sables (les ergs).

Le globe terrestre sera bientôt surpeuplé et trop petit pour le genre humain. Les denrées alimentaires font de plus en plus défaut. Les matières premières commencent à manquer. C'est pourquoi on pense à mettre en valeur le Sahara resté vide, improductif, jusqu'à présent. Ce sera la reconquête du Grand-Désert par l'homme.

Une industrie pleine d'avenir au Sahara est celle des transports, car il peut jouer le rôle d'une 'plaque tournante' entre le Nord, le Sud, l'Ouest et l'Est. Le chemin de fer transsaharien, appelé actuellement le Méditerranée-Niger, est commencé.

De plus, le Sahara procurera des bases précieuses à la navigation aérienne.

On a de grands espoirs de découvrir des richesses minières ou combustibles dans son sous-sol. Quelques-unes sont connues. Les prospections se multiplient. Presque chaque année de nouveaux gisements sont mis en exploitation.

Lorsque de grandes richesses minérales seront découvertes, il faudra réunir le nombre de travailleurs nécessaires aux industries extractives. On devra alors résoudre la question très bien définie par Henri Prat: 'Dans toutes les zones sèches, le problème de l'existence humain se pose ainsi: la population que l'on peut faire vivre en un lieu donné est directement fonction de la quantité d'eau que l'on peut fournir au sol. Tout doit donc y être subordonné au problème de l'eau, "facteur limitant" de toute activité humaine'.

La recherche des eaux du sous-sol dans le Sahara oriental est encore peu avancée. Il en est autrement dans le Sahara occidental, bien étudié depuis longtemps par les savants français. Il faut évoquer ici les étonnantes perspectives d'avenir qu'a ouvertes le géologue J. Savornin qui, dès 1927, a signalé l'existence d'énormes réserves d'eaux artésiennes exploitables surtout dans le Sud algérois. Cette exploitation est commencée.

Il est loisible, d'autre part, d'imaginer que les régions complètement dépourvues de nappe phréatique pourront, dans l'avenir, recevoir, par des pipe-lines, l'eau de lointains châteaux d'eau.

Enfin, il est permis de rêver que le progrès des inventions et la découverte de ressources énergétiques nouvelles apporteront un jour la solution du problème de l'eau au Sahara, par la transformation du climat.

Sous réserve des étroites servitudes imposées actuellement par la pénurie d'eau, comment espérer réunir au Sahara le nombre d'hommes qu'exige sa mise en valeur, les protéger contre un climat excessif, pourvoir à leur subsistance?

Trois éventualités peuvent être envisagées:

(1) Implanter des colons de race blanche
(2) Implanter des colons de race noire
(3) Recruter la main-d'oeuvre nécessaire parmi les habitants actuels du Sahara.

Ainsi se trouve posé le problème de l'acclimatement des races humaines en zône chaude et aride.

L'acclimatement n'implique pas seulement l'accoutumance de l'individu transplanté, mais encore la faculté, pour sa descendance, de se perpétuer, saine et vigoureuse, dans une longue suite de générations, sans croisement avec les Indigènes, et en conservant tous les caractères d'énergie physique et morale de la souche originelle. Sous l'expression de l'influence du climat, on a longtemps confondu deux phénomènes très différents: l'action du climat proprement dit, c'est-à-dire du froid et du chaud, de l'humidité et de la sécheresse, des circonstances atmosphériques en un mot, et l'action des maladies régnantes. C'est par un abus de mot qu'on englobe, sous la même expression d'acclimatement, l'adaptation aux conditions physiques, surtout météorologiques, d'un pays, et l'accoutumance à ses maladies infectieuses.

Du point de vue pratique, la question de l'acclimatement se pose donc en ces termes: (a) une race peut-elle s'adapter à une plus grande chaleur on à un plus grand froid que la chaleur ou le froid de la zone où elle a vécu depuis des siècles? Réponse: non, on ne se 'vaccine' pas contre le chaud ni contre le froid. Les techniques modernes permettent seulement de se protéger contre les excès de la température ambiante, par le 'conditionnement' du logement et du vêtement; (b) peut-on échapper à l'action néfaste des maladies exotiques? Réponse: oui, on peut, et l'on pourra de mieux en mieux, se défendre contre les maladies régnantes, par l'hygiène, la prophylaxie, la thérapeutique.

Les facteurs météorologiques excessifs du climat saharien éprouvent directement la physiologie de l'homme. Les réactions au climat saharien de la race blanche et celles de la race noire présentent des différences. Il convient de les considérer séparément.

Une des fonctions les plus importantes de l'organisme consiste à maintenir sa température normale. L'action de la température du désert, qui va de la glace à l'extrême chaud, exige un bon fonctionnement de la régulation thermique. Il y a incompatibilité physiologique entre la surchauffe permanente à laquelle le Blanc se trouve soumis au Sahara et le bon fonctionnement de ses organes. Plus ou moins et tôt ou tard, l'appareil thermo-régulateur, excédé, y fallit à son rôle. Les divers systèmes de l'économie sont alors troublés. Heureusement, une transpiration pro-

fuse vient sauver l'équilibre thermique. La sécrétion de la sueur, acte réflexe qui suit l'élévation de température, prend, au Grand-Désert, des proportions inusitées. La ration d'eau nécessaire est, par suite, fort élevée. Le chiffre minimum est de 5 litres par jour et par homme lorsque l'activité musculaire est restreinte et si l'on n'est pas exposé au soleil. En cas de travail un peu dur, il faut compter 10 ou 15 litres. D'autre part, les grandes transpirations soustraient à l'organisme du chlorure de sodium, ce qui n'est pas sans inconvénients, en particulier pour la sécrétion gastrique.

A la longue, les fortes chaleurs sèches provoquent des perturbations dans les fonctions digestives, mais c'est surtout sur le système nerveux du Blanc que le climat saharien exerce une action profonde: action exaltante chez les âmes de qualité, action dépressive qui peut devenir très dangereuse sur les esprits qui manquent d'équilibre.

L'influence néfaste de la sécheresse de l'air sur les enfants en bas-âge est bien connue. La mortalité des nourrissons blancs au Sahara est très élevée. On ne peut pas élever d'enfants blancs au Sahara. Les cimetières y témoignent de l'insuccès de quelques essais imprudents. La saison estivale surtout, qui dure de mai à octobre, leur est fatale, ainsi qu'aux femmes blanches fatiguées. C'est pourquoi le climat du Grand-Désert prohibe l'installation à demeure de familles blanches.

Il ne faut pas se laisser tromper par le fait que des Berbères blancs, les Touareg, sont fixés au Sahara depuis des siècles. En réalité, si les Tquareg sont arrivés à survivre, au Désert, c'est parce que leur fatigue physique est réduite: ce sont des pasteurs de troupeaux, des guerriers. Ils ne se plient pas aux durs travaux de l'agriculture.

En conclusion, les familles blanches européennes ou nord-africaines sont inaptes à l'acclimatement au Sahara: les hommes blancs peuvent venir y travailler, mais seulement dans les cadres. Ils ne doivent pas y être employés à des travaux de force. Ils ne doivent y être que des agents d'autorité, de commandement, d'encadrement, toutes personnes adonnées à un travail principalement intellectuel, et qui ne comporte pas grande fatigue physique.

Enfin, les Blancs que l'on veut transplanter temporairement dans le Grand-Désert doivent être l'objet d'une sélection attentive, portant sur les qualités physiques et morales, être installés dans des conditions de confort spéciales, pour le logement (qui doit être 'climatisé', au moins en ce qui concerne les cadres), le vêtement, la coiffure, et suivre des règles strictes d'hygiène et de prophylaxie. Les heures de travail doivent être bien calculées, et de longs congés en Europe ou en Afrique du Nord prévus.

Le Noir résiste mieux que le Blanc à la chaleur et aux rayons solaires, à cause de la pigmentation de sa peau et de sa rétine et du développement de ses glandes sudorpares. Mais le fait majeur est sa faible résistance aux basses températures hivernales, et à leurs écarts brusques. Il est plus sensible que le Blanc aux maladies *a frigore*. Cette sensibilité au froid rend le Noir inapte à fonder des lignées durables au Grand-Désert. La préhistoire nous donne une preuve de cet empêchement: les nombreux Néolithiques noirs qui peuplaient le Sahara au temps où il était

pluvieux et chaud ont reculé vers le Sud quand son climat est devenu aride, et frais en hiver. Le Noir n'est pas fait pour le Sahara. Si on veut l'y employer, ce ne peut être que comme travailleur saisonnier, temporaire, sans sa famille. On devra le vacciner contre la tuberculose par le vaccin B.C.G., et assurer sa surveillance médicale régulière.

Peut-on repeupler le Sahara en facilitant la multiplication et le développement des populations actuelles du Grand-Désert?

Deux sortes d'hommes vivent au Sahara: les hommes du palmier, c'est-à-dire les cultivateurs, habitants sédentaires des oasis, qui sont, presque tous, des Négroïdes, appelés Haratin — et les hommes du chameau, c'est-à-dire les pasteurs nomades dans les vastes espaces, qui sont de race blanche.

E. F. Gautier a dressé un tableau impressionnant de la misère trop fréquente des Négroïdes oasiens: 'Chez eux, ce qui frappe le plus l'oeil, d'abord, c'est l'abjection physique; ... la fièvre et la faim ont sculpté d'effroyables anatomies; ... Ces humbles échines de serfs font une impression de vie ralentie'.

Malgré leur misère, ces Négroïdes, adaptés à la vie sédentaire des oasis, y élevant leurs familles depuis des siècles, s'y livrant au dur travail de la terre, sont les seuls habitants du Grand-Désert qui peuvent fournir de la main-d'oeuvre pour sa mise en valeur. Mais leur nombre est insignifiant au regard des immensités qui entourent les archipels d'oasis. Leur accroissement numérique et leur développement physique dépendront de la quantité d'eau et du bien-être qu'on leur procurera. Il sera nécessaire avant tout d'élever leur niveau de vie, ce dont ces pauvres êtres sont incapables eux-mêmes.

A la différence des Négroïdes, sédentaires, les Blancs du Sahara, les 'hommes du chameau', berbères (Touareg), ou arabes (Cha'amba, Maures), sont en errance perpétuelle, de pâturage en pâturage dans l'immensité nue, avec leurs chameaux de selle ou de bât, quelques chèvres et quelques moutons à poils. Ils font soigner par des Haratin les dattiers qu'ils possèdent dans les oasis. La paix francaise a ruiné la principale industrie de ces nomades, qui consistait à prélever un tribut sur les Oasiens et sur les caravanes. Ils ne peuvent servir que comme 'gendarmes de désert' ou entrepreneurs de transport. On ne peut pas compter sur eux pour fournir des travailleurs du sol pas plus que du sous-sol.

Il n'y a pas de pathologie humaine spéciale au Sahara.

La grande pandémie des pays chauds et humides, le paludisme, n'existe, au désert chaud et sec, que dans les oasis. Les techniques antipaludiques issues des découvertes de A. Laveran et de R. Ross en ont facilement raison.

Le trachome est une grande plaie des oasis. Il y atteint, encore aujourd'hui, la grande majorité des nourrissons avant la fin de leur première année. Le meilleur moyen de lutte consiste dans une organisation de soins, locale et permanente.

Les Noirs sont très sensibles à la tuberculose, dont les formes pulmonaires évoluent très vite chez eux. La seule méthode de vaccination antituberculeuse par le B.C.G. des populations dispersées du Sahara est la méthode de Foley et Parrot, qui consiste à vacciner par scarification cutanée, sans épreuve tuberculinique préa-

lable, tous les enfants au-dessous de 15 ans en bon état apparent de santé – et dans la répétition des mêmes séances tous les 3 ans, dans le même lieu.

Les Noirs présentent une sensibilité très grande aux pneumococcies, à la méningite cérébro-spinale.

La bilharziose, qui est endémique dans le Sud marocain et dans le Sud tunisien, comme en Egypte, a tendance à envahir d'autres oasis du Sahara occidental.

Les piqûres de scorpions constituaient un redoutable danger dans beaucoup d'oasis, où les cas de mort n'étaient point rares. Le 'péril scorpionique' peut être écarté depuis que l'Institut Pasteur d'Algérie prépare un sérum antiscorpionique efficace.

En résumé, le Sahara, pluvieux et habité à l'époque paléolithique, s'est dépeuplé lorsqu'au Néolithique son climat est devenu aride et excessif. Actuellement, le Sahara, qui couvre 8 millions de kilomètres carrés, ne compte que 3 millions d'habitants: moins d'une demi-unité par kilomètre carré. Comment le repeupler?

(1) *Par l'immigration de Blancs?*

L'acclimatement de familles blanches est impossible au Grand-Désert, parce que les femmes et surtout les enfants ne peuvent pas supporter la chaleur, la sécheresse et les vents torides de l'été, durant 5 mois.

Les hommes blancs, sans leur famille, peuvent vivre temporairement au Sahara, à condition d'être sélectionnés, d'avoir du confort et d'observer les règles de l'hygiène. Les Blancs peuvent être employés dans les cadres (Européens et Nord-Africains), et, jusqu'à un certain point, pour des périodes limitées, comme manoeuvres saisonniers (Nord-Africains célibataires).

(2) *Par l'immigration de Noirs?*

L'acclimatement de familles noires est impossible au Sahara, à cause des refroidissements hivernaux et des brusques écarts de la température.

Les hommes noirs, sans leur famille, peuvent fournir des travailleurs saisonniers (actuellement des manoeuvres ou des ouvriers), à condition d'être sous surveillance médicale.

(3) *Par la multiplication des Indigènes actuels?*

Les Oasiens Négroïdes, qui sont déjà adaptés au climat, peuvent faire souche au Sahara, mais leur existence est misérable. Leur multiplication sera proportionnelle à la quantité d'eau qui sera mise à leur disposition et conditionnée par le relèvement de leur niveau de vie. Ils peuvent fournir une main-d'oeuvre sédentaire.

Les nomades, chameliers Blancs, arabo-berbères, pasteurs errants et anciens pillards, n'ont ni le désir ni la possibilité de se livrer à un travail manuel; tels qu'ils sont, ils sont incapables de prospérer dans un pays pacifié et policé.

En conclusion, sous le climat actuel, le *peuplement* proprement dit du Grand-Désert ne pourra être réalisé que par les familles des Oasiens Négroïdes, dans la mesure où l'eau vitale et une alimentation suffisante leur seront assurées. Pour la

mise en valeur et l'*exploitation* des richesses du sous-sol et des voies de communication, les Blancs de race pure et les Noirs de race pure ne peuvent être au Sahara que des travailleurs passagers, fournissant des cadres et de la main-d'oeuvre temporaires, sans implantation de leurs familles.

Pour diminuer les efforts physiques, épuisants au Désert, de la main-d'oeuvre, dans les industries extractives, il faudra recourir le plus possible à la mécanisation, et, pour cela, disposer de ressources énergétiques.

PHYSIOLOGICAL EFFECTS OF COLD ENVIRONMENTS ON MAN

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The problem of mammalian, including human life in cold environments is essentially a problem of insulation. Warm blooded animals, apart from periods of hibernation, maintain a relatively constant deep body temperature of approximately 37°C with an outer shell of tissue, the temperature of which depends on the thermal environment and the state of activity of the animal. The constancy of the internal temperature depends on a balance of heat output and heat loss. Scholander, Irving and their colleagues, who have recently published an important series of studies on arctic animals, point out that there are three ways by which such animals might develop mechanisms for survival in extreme cold. There might be a fluctuating deep body temperature, varying according to external temperature. Their evidence strongly discounts such a possibility: arctic animals, such as the fox or the dog, maintain a constant deep body temperature of the same order as temperatures found in animals inhabiting temperate or tropical zones. There could be an increased heat production, i.e. a high metabolic rate. Scholander and Irving do not consider that that is an important factor as the basal or resting metabolic rates in a large variety of arctic animals showed the same relationship to surface area as demonstrated by animals living in tropical or temperate zones. The points fall close to the 'mouse-elephant curve' constructed by Benedict many years ago.

The third mechanism consists of variation of the insulation of the deep body temperature. This in turn depends on the thickness of the subcutaneous layer of fat, the rate of blood flow in the skin and superficial tissues, the rate of production of water on the surface of the body, and the thickness of the fur. In their experience Scholander and Irving found that maintenance of a constant deep body temperature in arctic animals depended essentially on adequate insulation, and this in turn was largely due to the thickness of the layer of fur.

How does man adjust physiologically to life in cold environments? Is there any evidence of relatively long term effects which suggest acclimatization to cold? It should be made clear, at the outset, that the evidence so far is meagre, and there is certainly no such dramatic effects as are observed when man is exposed to hot environments, as described by Dr Weiner.

The critical temperature for a nude man at rest is relatively high, about 27°C. That means that body temperature is maintained without any change in metabolism, down to temperatures of 27°C. Thereafter any further fall of environmental temperature will stimulate an increased metabolism. This may be compared with a critical temperature of −40°C for the arctic fox.

Metabolic rate, i.e. heat production or oxygen consumption, starts to increase when the environmental temperature falls below the critical temperature. The increased heat production is largely or possibly entirely due to shivering or other muscular activity. The rise in metabolic rate may be very considerable and for short periods can be as high as 6-7 times the resting or basal metabolic rate, i.e. up to

300 cal./m^2/hr. These high rates cannot be maintained for long periods and the ave-average increment over a period of one hour is unlikely to exceed 150-200 cal./m^2/hr.

If the cold environment is maintained, shivering gradually diminishes as exhaustion proceeds and the deep body temperature will begin to drop. When body cooling is accelerated by immersion in cold water, it is found that shivering ceases at a rectal temperature of approximately 32-33°C, and metabolic rate declines thereafter with rectal temperature. Conciousness is lost at a rectal temperature of 30°C and death usually occurs at rectal temperature of 25°C, although survival has been reported in one subject whose rectal temperature was below 20°C.

There are many other physiological changes which occur during acute exposure to cold which can only be briefly summarised. The effect is to diminish heat loss by increasing insulation, which is mainly effected by vasoconstriction in the skin and underlying muscles. The reduction in blood flow leads to a fall in skin temperature, and the gradient of temperature from the deep tissues to the surface becomes steeper. Body hair is vestigial in man, but the pilo-arrectores muscles attached to the roots of the hairs contract and so produce goose flesh in the skin. This roughening of the skin surface increases the boundary layer of air in contact with the body and so has a small effect on insulation. Water loss from the skin surface is greatly reduced.

Acute exposure to cold also stimulates certain endocrine changes, similar to those described by the term 'alarm reaction'. The main characteristic of this reaction is the increased activity of the adreno-cortical mechanism.

The effects of long continued exposure to cold environments include vascular and endocrine changes. As a result of peripheral vasoconstriction, there is a shift of blood from the superficial regions of the body to the pulmonary and probably the splanchnic areas. In addition, there is a gradual diminution of the blood volume, owing to the loss of plasma with consequent hàemoconcentration. The proportion of red cells to plasma increases from a normal of 46% up to 52-55%. During the period of haemoconcentration there is a marked increase of urine secretion, and this diuresis represents a period of increased water loss.

The endocrine changes in man cannot be adequately described at present. In laboratory animals who are exposed for long periods to temperatures of 0°C, there is an increased activity of the thyroid gland, which is accompanied by a gradual rise in the basal metabolic rate.

In laboratory animals there is also a hypertrophy of the cortex of the adrenal gland, which can be diminished by increasing the amounts of ascorbic acid in the diet.

The main physiological problem as far as man is concerned is whether acclimatization to cold takes place, in the sense that physiological changes occur which increase tolerance for cold or improve survival in the cold. Such changes can be clearly demonstrated in laboratory animals. Blair, for example, has recently compared the responses of control rabbits with animals kept in the cold chamber for many weeks. When both were exposed to very severe cold, the control animals all

had severe falls of body temperature whereas the cold adapted ones maintained a steady body temperature. After removal all the controls developed frostbite, but there was none in the treated animals.

Much work has been done in recent years to investigate the possible development of acclimatization in man, but the positive findings are few. There have been a number of studies on the Eskimos, who are the best example of people adapted to life in severe cold.

The most comprehensive enquiry has been that of the Queen's University, Kingston Ontario, under the direction of Dr Malcolm Brown. A group of workers have spent several summers in Southampton Island, which is north of Hudson's Bay, latitude 65°N, investigating physiological, nutritional, medical and social aspects, and the work is still in progress.

The basal metabolic rate of the Eskimo is raised, averaging 30% above normal values for the temperate zone (Hatcher, 1950). Similar raised B.M.R.'s in the Eskimo had been recorded earlier by several workers, but the figures have not always been accepted, as the conditions of measurement were subject to criticism. The work at Southampton Island appears to be free of criticism as a number of repeat determinations were made over a period of several weeks and the measurements were made in the Eskimos' huts or tents after a period of at least 8 hours asleep and before arising from bed. So it appears probable that there is a true increase in the B.M.R. in the Eskimo.

There is no evidence as yet that other people who live in the north develop an increased B.M.R. but not many comparable studies have been carried out. Such work has been attempted on Antarctic expeditions, without any clear results indicating a rise, but this may have been due to the difficulties of measurement. On the present British North Greenland Expedition a physiologist will be carrying out regular determinations, and as the members of the expedition will remain in arctic regions for at least a year, it is possible that satisfactory evidence for or against an increased metabolic rate in the cold will be obtained.

Peripheral blood flows were measured in the forearm at various temperatures in the Southampton Island Eskimo and the values were closely similar to those obtained in similar experiments in this country. There were, however, two possible exceptions Water temperatures ranging from 10°C to 45°C were used in this country, 45°C being the highest temperature which can be tolerated for periods of two hours. The Eskimos were unable to keep their arms in water at 45°C as blisters developed on their fingers.

At the other end of the temperature scale, it appeared that average blood flow in the Eskimo, when the arm was immersed in water at 10°C, was significantly higher than in similar experiments in this country. Although these results are very suggestive, it is clear that further experiments are needed.

There are many references in the literature on the Eskimo which indicate an improved tolerance to cold especially in the hands, such as ability to handle cold

objects or to carry out manipulations which would be impossible for the white man. There is also clear evidence by Mackworth that local adaptation to cold in the fingers can be developed by continued exposure. Mackworth measured the duration and degree of finger numbness by changes in tactile discrimination during and after exposure of the bare finger at various temperatures and wind speeds. He carried out his first experiment at Fort Churchill and found a significant difference between indoor and outdoor workers; the latter have less and shorter impairment of finger numbness with similar exposures than the former. As the results might have been interpreted as indicating an ability to discriminate with fewer sensory clues by practice, i.e. a cortical rather than a local change, Mackworth also carried out experiments at Cambridge. A number of subjects spent two hours a day in a room, the temperature of which was kept at $-10°C$. They wore ordinary seamen's clothing, with bare hands. After two hours, one finger was exposed to a blast of cold air and tactile discrimination was measured. The rest of the day was spent in normal activities outside the chamber.

During the first two to three weeks the finger numbness steadily diminished and thereafter kept at a steady level. This result was not due to a learning factor as shown in another experiment in which the subjects only spent one hour a day in the cold room. No decrease in the numbness index was obtained under these conditions. This experiment is an important one as it is the best objective evidence of significant acclimatization to cold. Studies on the vasomotor changes are not yet complete.

The fishermen of Nova Scotia who habitually have their hands in cold water also exhibit a degree of adaptation. When the hands are plunged into the water, the normal individual suffers considerable pain, with a sharp rise of blood pressure. This is the basis of the cold pressor test used in clinical medicine as a test of actual or potential hypertensive subjects. The fishermen experience no pain and no rise of blood pressure on immersing their hands in ice water.

Other factors which were investigated by the Queen's University group included the nutrition of the Eskimo. It is commonly supposed that this dietary consists of a high fat, high protein and low carbohydrate content. The difficulties of determining the average diet is very considerable owing to the very wide daily and individual variation both in composition and calorie value. Within a single week the daily intake of one individual varied from 2,000 - 6,000 calories. On one occasion 80% of the calories might be derived from fat, on others it might be as low as 10%. The raw material of the food was available ad libitum, but it appears likely that the very erratic feeding habits are related to the more normal situation in which food supplies are dependent on successful hunting and hence are extremely irregular.

As a result of many dietary experiments in relationship to cold, it has been shown that calorie requirements are considerably increased in the cold. In temperate zones the diet of the soldier provides approximately 3,300 calories. At Fort Churchill the rations issued yielded 5,000 calories. Part of this increased metabolic demand is due to the hampering effect of arctic clothing, and it is not completely certain if there is a true metabolic increase apart from this.

High fat, high protein and high carbohydrate diets have been compared in experiments with subjects who lived for long periods in cold chambers. Cold tolerance was highest on the high fat diet, although the high carbohydrate diet was almost as good. High protein diet was markedly inferior. Mitchell, Gluckman and their colleagues, who were responsible for these experiments, suggest that the high fat diet may owe its value to the laying down of fat in the subcutaneous tissue.

The thickness of the subcutaneous layer of fat can be of considerable importance as regards insulation. The thermal conductivity of human fat is from ½ - ⅓ that of muscle. The difference in conductivity within the body may be even greater as muscle is a much more vuscular tissue than fat. Recently my colleagues Dr Pugh and Dr Hatfield have investigated the effects of immersion in cold water, and were particularly interested in the performance of long distance swimmers. During the last war considerable information was obtained of the survival at sea of shipwrecked sailors. Molnar collected this information and his figures showed the time during which survival was likely at various sea temperatures. His figures suggest that at a water temperature of 15°C, there would be few survivors after five hours' immersion. On the other hand, Channel swimmers may spend from 10 - 20 hours in the water, and measurements made last year during the race across the Channel showed that the water temperature, except along the coasts, was approximately 15°C. Observations were made on a number of the competitors in this race, and one volunteered for further experiments. All the competitors examined were extremely fat with a subcutaneous layer up to three times that normally expected. Comparisons were made of the rate of cooling of the Channel swimmer and control subjects. In well stirred water kept at 15°C normal subjects shivered violently and the oxygen consumption rose up to seven times the resting rate. In spite of the violent shivering, rectal temperature fell and one subject had to be removed after 40 minutes. The swimmer, on the other hand, remained lying in the water reading a paper, with only very mild shivering and quite comfortable. His metabolic rate was only doubled and there was no fall in rectal temperature. From studies made of the tissue gradients it was clear that the great difference was largely explained by the insulation of the subcutaneous fat.

It is possible, therefore, that the high calorie, high fat diet, which is preferred in cold regions, may owe some of its value to the increased development of subcutaneous fat.

The mechanisms which may be responsible for increased tolerance to cold, developed during long exposure to cold,can include a small rise in basal metabolic rate, a changed distribution of blood permitting a greater constriction of peripheral vessels, an increased insulation provided by fat, and a diminished local effect of cold, the mechanism of which is as yet unknown.

The greatest and certainly the most important adaptation to cold environments is not these relatively small physiological adjustments but learning how to live in arctic conditions. The insulation required is provided by clothing, the absence of cold injury is due to the avoidance of risks, and a knowledge of the conditions

likely to cause accidents. It is quite easy to detect early frostbite on exposed parts, such as the cheeks or nose, and to rewarm such areas merely with the fur on the back of gloves without any damage or discomfort.

Life in cold climates is perfectly tolerable once the rules are obeyed.

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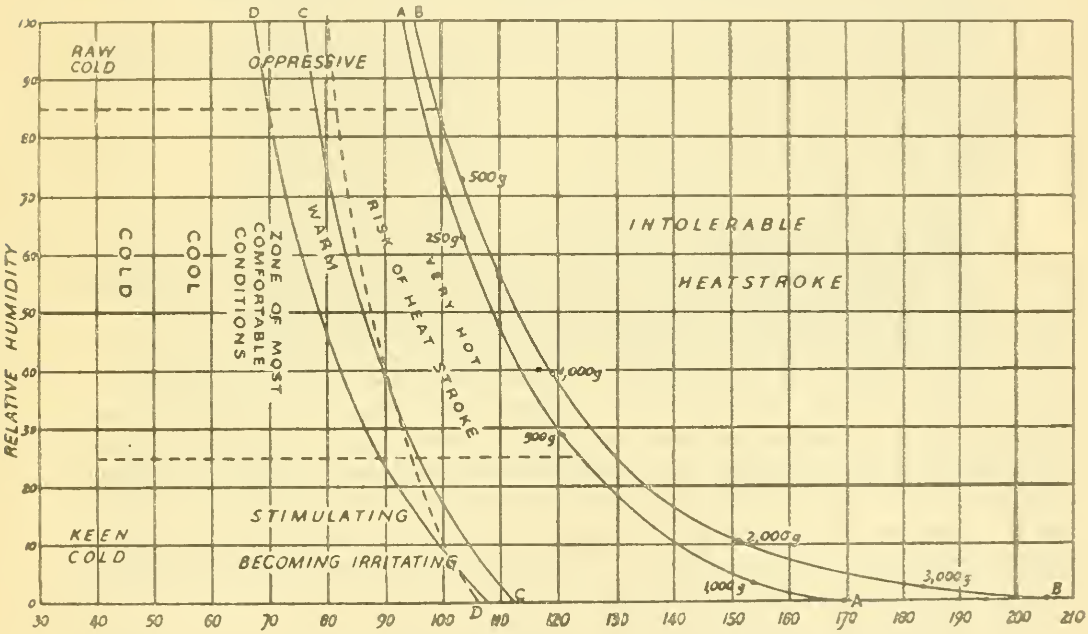
SOME ASPECTS OF HUMAN ECOLOGY IN HOT TROPICAL REGIONS

Professor Sir David Brunt, Sec.R.S.

(London)

I have always been attracted to that aspect of physiology which deals with the relation of man to his physical environment, by the hope of finding some logical basis for the classification of the climates which occur in different parts of the globe. In Fig. 1 below is reproduced a diagram* in which is given a tentative classification of climates, which I had hoped to test by comparison with data of times of day and year when work of a specified degree of activity became impossible. The line CC was assumed to be the limit to the right of which outdoor work would be try-



(by courtesy of the Physical Society).

Figure 1.

AA. Heat-stroke limits for nude man resting in still air.

BB. Heat-stroke limits for nude man resting in air moving 200 ft/min.

CC. Limiting conditions for clothed man resting in sunshine with about one-third of skin wetted with sweat.

DD. Limiting conditions for clothed man walking 3 m.p.h. with about one-third of skin wetted with sweat.

The broken line represents equivalent temperature 80°F. The figures 500 g, etc., indicate rate of evaporation of sweat in grammes per hour for men of average size in order to maintain heat balance of the body.

* from Brunt, D. 1947. Some Physical Aspects of the Heat Balance of the Human Body, *Proc. Phys. Soc.*, **59** 713.

ing, or in extreme cases impossible, but it has not been possible hitherto to test the truth of this supposition. Through the courtesy of Mr D. A. Davies, Director of the East African Meteorological Department, climatological data for his area, and a statement of the hours of office work in certain parts of Africa, have been supplied to me.

The statement concerning hours of office work is as follows:

A Uganda and Tanganyika (including Lake Area) – Normal office hours with 1½ hr lunch break.

B Kenya Highlands and East of Rift – Normal office hours.

C Rest of Kenya – Normal office hours with 2 hr lunch break, except that sometimes in Northern Province Area there is no afternoon work.

D Zanzibar and Pemba – No work in the afternoon.

The following stations were selected as characteristic of each of the four areas:

A Kitgun
B Nairobi, Nakuru
C Mombasa
D Chukwani

The data were represented in a diagram as in Fig. 2, the monthly mean of the daily maximum temperature being plotted against the monthly mean of the daily minimum relative humidity, which will be approximately synchronous, except that for Chukwani the 15h mean values are plotted. It was thought that observations from Area A (Kitgun) should be about marginal between conditions possible and impossible for afternoon work, and that in Fig. 2 points representing area B should fall to the left of those for Kitgun, and those representing areas C and D should fall mainly to the right of those for Kitgun. Fig. 2 only shows observations for Kitgun, Nairobi and Chukwani, the other stations selected for insertion being left out for the sake of clarity. A number of places in area B (e.g. Nakuru) were represented in Fig. 2 by points to the left of the strip covered by the Nairobi observations and so were not retained in the final form of the diagram.

Area D, where no work is done in the afternoon, is represented by Chukwani in Fig. 2. The points representing monthly values for Mombasa, where there is a 2 hr lunch break, fall so closely within the same area as those for Chukwani, that they were omitted. The line CC which has been drawn in Fig. 2 is the line CC of Fig. 1, and it appears to give as good a fit as can be expected for the marginal conditions represented by the observations.

The view that CC is a boundary having some practical value is put forward in the hope that either further confirmation will be available, or other observations are available which show that this boundary requires revision. There must be some such boundary for work of any specified degree of activity and it is an important matter to obtain as close a specification as possible.

I will assume for the rest of this paper that I am correct in using CC as a boundary such that conditions represented in the area to the right of CC will make it im-

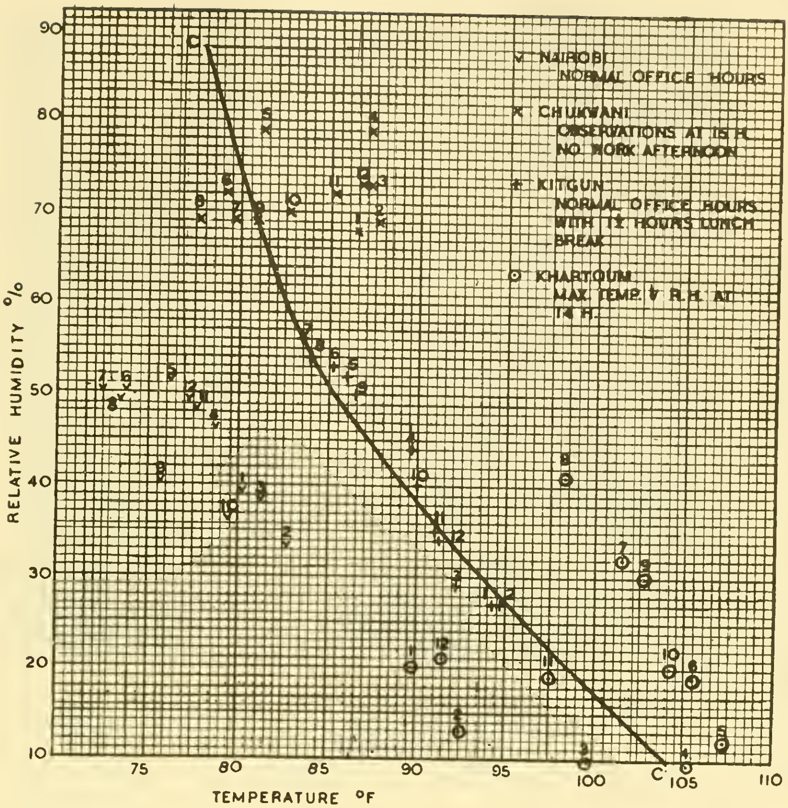


Figure 2.
Monthly mean values of maximum temperatures (daily) and daily minimum of relative humidity

possible to do even light work out-of-doors. If the relatively frequent occurrence for 3-4 hours per day of conditions hotter than correspond to the line CC is to be avoided, the mean temperature of the hottest month should not exceed 75°F in a dry climate, or 73°F in a damp climate. This rule may be taken as a rough guide.

At Beira on the Coast of Portuguese East-Africa, slightly north of latitude 20°, the monthly mean values of minimum relative humidity vary between 59 and 63%, the monthly mean maximum temperatures varying from 77.3°F to 89.6°F. All the months from May to September are to the left of CC in Fig. 2, all the remaining months being to the right of CC. Thus it is likely that normal office hours or light work out-of-doors, would be possible from May to September inclusive, but would not be possible during the remainder of the year.

Among the data which I received from Mr Davies from East Africa were hourly mean temperatures and relative humidities for each hour of the day, and month of the year, for Chukwani. From these data it is possible to represent, on such a diagram as that shown in Fig. 2, the mean diurnal variation of the conditions for each

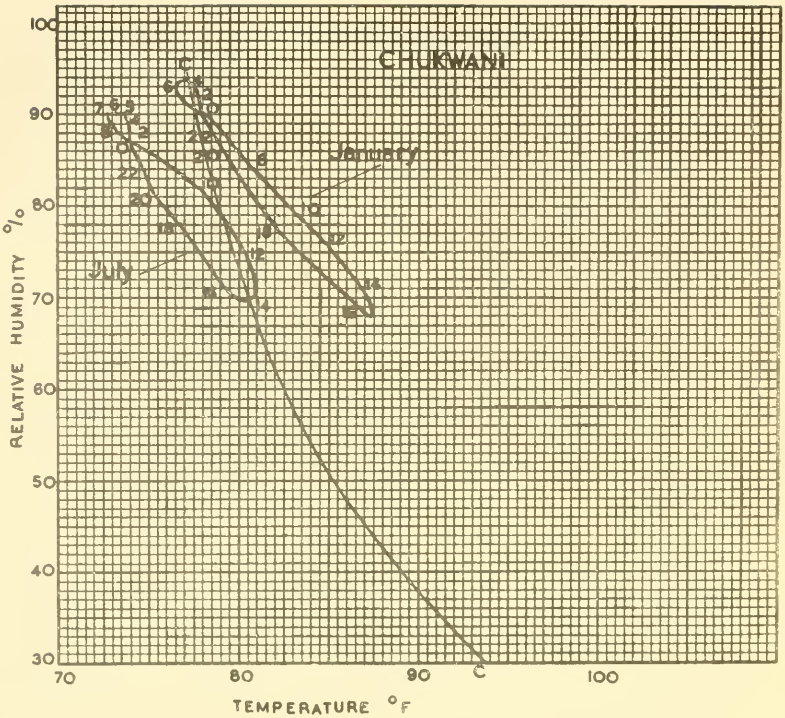


Figure 3.
Mean diurnal curves for January and July

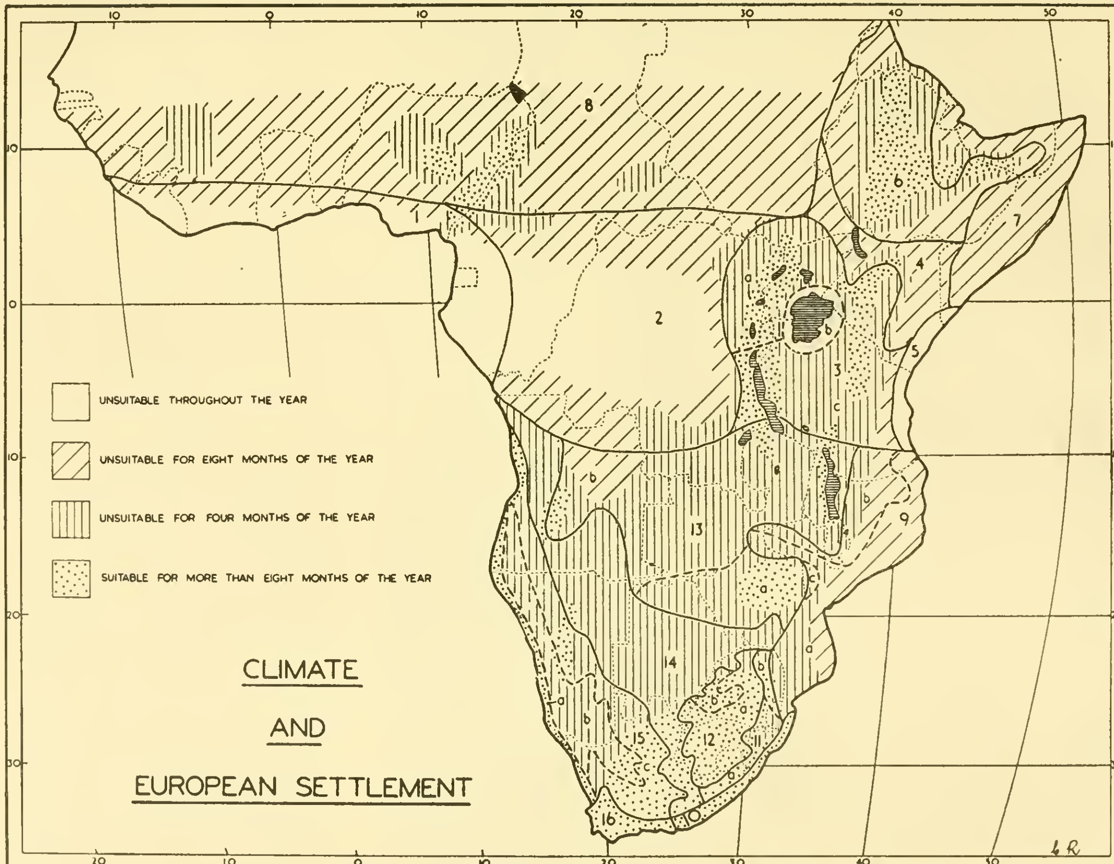
month of the year. Such a representation is shown in Fig. 3, for the extreme months January and July, which are the hottest and coolest months respectively.

From Fig. 3 it may be concluded that at Chukwani in January light outdoor work is likely to be impossible during the whole day, while even in July work is likely to be impossible during the hours of the afternoon.

If such a diagram is drawn for each month of the year, for any place, we can from these come to a conclusion as to the number of months of the year in which work is possible during the day. From Fig. 3 it seems safe to conclude that Chukwani is not a pleasant place for the white man to settle in.

Data for Khartoum are also shown in Fig. 2, and appear to indicate that in the months from May to October active work is likely to be trying for the white man during the afternoon. That this is true is confirmed by Mr J.F. Ireland, the Director of the Sudan Meteorological Service.

The method outlined above in Figs. 2 and 3 can readily be applied to relate the problems of white settlement to climatological conditions. My friend and former pupil Dr S.P. Jackson, of the Department of Geography at the University of the Witwatersrand, has carried this method of analysis to its logical conclusion and has given a map of Africa south of about latitude 12°N, on which is indicated those



(by courtesy of the Oxford University Press).

Figure 4.

Climate and European Settlement South of the Sahara.

parts of Africa which are unsuitable for European settlement (a) throughout the year, (b) for eight months of the year, (c) for four months of the year, or (d) suitable for more than eight months of the year.

When a diagram such as Fig. 3 shows that four hours of the day in a particular month fall to the right of the line CC, it is concluded by Jackson that the place in question is unsuitable for Europeans during that particular month. The work involved in drawing such a map as that shown by Jackson is completely straightforward, and requires only reliable values of temperature and humidity for each hour of the 24 in the day. His map for regions south of the Sahara is shown in figure 4.

Dr Jackson's work is, as he himself states in the publication referred to*, only a first approximation. It does not take account of winds, nor of the possible effects of a long stay in a monotonous climate, which is regarded by some writers as having a serious effect in leading to a loss of initiative and efficiency.

In the brief statement above, I have endeavoured to show the vital need to make use of the fact that in some parts of the globe active outdoor work is only possible during some hours of the day, or during some months of the year. There is a great need to collate records of the hours when work is possible with the meteorological records available, and possibly to institute new meteorological stations in regions as yet unprovided with records. I should regard such collation as a most useful addition to the knowledge we have acquired by laboratory experiments on human subjects in controlled atmospheric conditions.

I have asked that the African Regional Association of the World Meteorological Organization should discuss this matter at their forthcoming session in January 1953, with a view to considering what information they can supply. If any information can be obtained by this means, or by any other means, I should be glad to do the work of reducing and discussing such observations.

* Jackson, S.P. 1951. Chapter 1 in: *Africa South of the Sahara.* Oxford University Press.

DISCUSSIONS

Session I.

CLIMATE AND PHYSICAL ENVIRONMENT

Chairman Dr Edward Hindle, F.R.S.

In the discussion that followed the first session, Professor J.A. Prescott, F.R.S. said that there was no nomadism in Australia, but that cattle moved to new green areas after each thunderstorm. There were no fences in Northern Australia to restrict their movements, and permanent water-holes were kept as a final reserve: Canning stock routes had been used only once since their establishment and were difficult to maintain. The scattered nature and local distribution of rainstorms had long been recognized by pastoralists engaged in cattle rearing on the tropical margins of the Australian deserts, and played a part in determining the size of 'paddocks'. Cattle moved towards more favoured areas during the dry season and would be stopped by fences.

Considerable experience had been gained in Australia on the use of water for irrigation, stock and domestic purposes. In the neighbourhood of Adelaide water containing 800 parts per million total salts was regularly used for irrigation and was supplemented by 20 inches of rain falling in winter. Probably the longest record of the satisfactory use of such water for irrigation came from Siwa Oasis where waters containing 2,000 parts per million of salt had been in use. An extraordinarily efficient drainage system had made possible an unusually permanent irrigated agriculture. In Southern Australia the search for underground waters was of lively interest to the Department of Mines and Geological Survey. The existence of overlying saline ground waters was frequently observed, and attempts were made to avoid mixing these with fresh water from lower levels.

Asked whether water could be de-salinized chemically, Professor F. W. Shotton replied that the operation was costly, required skilled supervision and was therefore not practicable, but Dr H. Boyko said that methods were being investigated at Harvard and the Weizman Institute. Another speaker pointed out that in hot climates saline drinking water was desirable, and Dr N. Wright enquired about the adequacy of geological knowledge. Professor Shotton agreed that such knowledge was still inadequate and that the details were largely unknown. Although the quality of underground water could not be determined in advance, geophysical methods could increase the proportion of productive borings. Dr C. B. Williams asked about the wells at Fuca, and Professor Shotton answered that there had been two native wells there.

Mr J. Tosic said that a distinction must be drawn between 'free' and 'bound' water in the analysis of desert soil samples, and Mr H. Green pointed out that irrigation was associated with a stable system of agriculture but that there were transitional stages leading to nomadism. The flood waters of the Nile did not follow precisely the same course each year. The inland deltas of the Gask and Barak rivers in the Anglo-Egyptian Sudan and Wadi Bana at Aden each year received violent

spates of water containing so much sediment that storage by means of dams was impracticable. Deposits caused a rise in the level of the river bed and this natural rotation of the soil reduced weeds. The cultivator had the advantage of using the equivalent of virgin land where the ground was watered only once in four years because pests were eliminated. Nomads noted the direction and duration of storms before deciding where to cultivate. It was important to see that water was not consumed by unwanted vegetation. Near Khartoum, where there were only a few inches of rain annually, mosquito trees had been established on sand dunes by planting them at shallow depth in moist sand and removing the inconspicuous weeds. Similarly nomads guarded their lands from trespassing herds. Dr Williams then pointed out that the frequency of the distribution of rainfall was on a logarithmic scale.

Professor J. F. Danielli asked why alkalinity was so serious and Professor Prescott replied that sodium carbonate made the soil impermeable and no crops could tolerate an alkalinity above pH. 10.0.

Session II

PLANT ECOLOGY

Chairman Dr B. T. Dickson

Professor F. W. Shotton asked whether the artesian water of the Bahrain Islands originated from Central Arabia and Professor R. D. O'Good answered that such was the local opinion. The water was believed to flow northwards towards the Persian Gulf. Professor F. S. Bodenheimer said that between the times of aestivation and hibernation there was a short, favourable period during which it would be fatal for plants and animals to become active. Only in spring was the favourable period long enough for development. Professor M. Zohary agreed, and added that the Middle East Deserts belonged climatically to Africa rather than Asia.

Dr C. B. Williams enquired about the possible hygroscopic value of the salt crystals that encrust many desert plants, but Professor D. Thoday said that plants could not absorb water from them. Professor G. E. Blackman said Professor Zohary's measurements were all of dry weight and asked why he had given no measurement of transpiration from unit areas. The latter replied that surface measurement in desert plants in the spring was open to many errors.

Session III

ENTOMOLOGY AND ECOLOGY

Chairman Dr J. W. Evans

Referring to Professor F. Bernard's paper Mr D. Wragge Morley said that the more primitive ants were nearly always insectivorous while the more highly developed species were omnivorous and protected scale-insects, aphids and other harmful plant-sucking insects. At the same time the more primitive ants, like *Cataglyphis* could not compete with the social *Monomorium*. The latter and similar 'harm-

ful' ant species required conditions in which agriculture was possible while the hunting *Cataglyphis* were not so dependent on well-established vegetation and were therefore to be expected on the desert fringes and gave way to more social species in agricultural areas. It was not however true to say that the ants which protected plant-sucking insects were invariably harmful. The activities of ants in turning over and aerating the soil might be of special importance in cultivated areas near deserts. In Brazil for example where there were no earthworms, it had been calculated that ants brought to the surface nearly a third as much soil again as that brought up by earthworms in Europe.

Mr R. M. Elton referred to the importance of insects as human food and mentioned that he himself had sampled 43 species in Africa and Australia. Many such as the witchetty grub contained a large proportion of moisture and their high salt and glucose content enabled the natives to travel long distances on this diet in hot, dry deserts.

Professor A. Balachowsky said that crows were never to be seen feeding on date-palms in the Sahara, but that in their search for ticks they sometimes injured camels and were therefore shot when seen on the backs of these animals.

Professor F. S. Bodenheimer emphasized the vulnerability of crops in oases both to insects that changed their food habits, and to all the animals which attacked plants for the sake of moisture.

Dr C. B. Williams pointed out that the North African desert was one of the routes by which insect migrants travelled to Europe and that they bred along the fringes of the desert. This area was also the main breeding-ground of many insect pests whose numbers varied according to the rainfall. Similar conditions occurred in North America.

Mr H. Green suggested that Professor L. Emberger had not sufficiently emphasized the skill required by an ecologist before he could safely interpret his observations and make them a guide in land use. Conditions were radically altered by irrigation and fencing, pest control and the use of fertilisers or trace elements. Consequently the ecologist's inferences involved a large subjective element of skill and experience and an appreciable chance of error.

Dr H. Boyko also said that the interpretation of ecology to agriculture was skilled work and often man obtained less from the land than it could support naturally.

Session IV

ECONOMIC ASPECTS

Chairman Dr H. G. Thornton F.R.S.

In reply to a challenge for evidence that forest clearance resulted in reduced rainfall, Professor E. P. Stebbing said that during their advance into India, Alexander and his army had marched through vast areas of virgin forest where now only desert was to be found. Professor J. F. V. Phillips added that during the last 150

years aridity had definitely increased in the eastern part of Cape Province and Northern Transvaal following the removal of evergreen forest. Although it could not be proved that tree planting increased the rainfall or that forest clearance reduced it, the availability of water was certainly increased by the presence of trees.

Commenting on Professor Stebbing's remarks, Dr A. S. Thomas said that a deep humus layer was seldom to be found in tropical forest: indeed there was usually more organic matter in grassland soils. He did not believe that fire had a deleterious effect on grassland – the worst factor was compacting of the soil surface by stock animals. Tramping had produced desert-like conditions in Karamoza where there was an annual rainfall of 25 inches. When tse-tse fly invaded the land however, and the stock went away, the vegetation soon recovered. He agreed with Professor Phillips that tse-tse had a beneficial effect in preserving Africa.

Fire was a useful agent in the right place and at the right time, provided that the ground was allowed to rest afterwards, said Professor Phillips: and much had been learned about mechanized agriculture from experience in Tanganyika. The removal of deciduous scrub at Kongwa had not resulted in a 'dust-bowl' or 'tennis court'; and acres thrown back to nature had produced a crop of grass at the end of a year. Africa needed a few years to rehabilitate herself he suggested.

The impossibility of countering the rape of the earth by overgrazing, when the entire population was clamouring for food, was mentioned by another speaker with experience of the problems in Somaliland Protectorate.

The paper by Professor H. C. Trumble and Mr K. Woodruffe was presented by Professor J. A. Prescott, F.R.S. in the absence of the authors. In a short introduction, the latter said that the University of Adelaide possessed two field stations in the semi-arid fringe to the southern margin of the Australian desert. Koonamore dealt with the natural regeneration of native shrub steppe and was in charge of the School of Botany. Yudnapinna had been endowed since 1938 for the special study of pastoral management in this environment and was the responsibility of the Waite Agricultural Research Institute. There had been pastoral occupation in the regions for nearly one hundred years, and overstocking with sheep during drought periods had resulted in an estimated loss of 80% of the original perennial shrubs. It was expected that these studies by the Waite Institute would lead to a basis for the establishment of scientific principles of pastoral husbandry.

In the discussion following the paper, Dr H. Boyko enquired about competition between bushes and grasses in areas where *Atriplex* and *Kochia* were the dominant plants. This was a subject of very great importance in large areas of North America. North Africa and South-west Asia. In North America *Artemisia tridentata* covered large areas as a result of overgrazing. He had recently seen large scale experiments from Montana to Texas that were designed to establish methods for controlling this undesirable shrub. In North Africa and South-west Asia, a related species *A. herba alba* covered nearly the whole area between the isohyetals of 200 and 400 mm. from Morocco to Afghanistan where there were cool winters. The latter

species however had a root system providing much weaker powers of competition. After the elimination of grazing for a number of years good fodder grasses could easily compete with it. This was because the rainwater was absorbed by the fibrous root system of the grasses before reaching the deeper top-roots of the *Artemisia.*

Session V

MAMMALIAN PHYSIOLOGY AND ECOLOGY I

Chairman Professor A. V. Hill, F.R.S.

Dr Edward Hindle, F.R.S. referred to the work of Dr H. B. Cott who had shown that the dark colours of some desert birds were a protective mechanism, since these were unpalatable. Professor J. F. V. Phillips drew a parallel between Dr N. Wright's fat-tailed sheep and the 'fat-tailed' bushmen of the Kalahari and Karoo deserts. He agreed that the selection of indigenous sheep and goats was most important. Professor F. S. Bodenheimer said that a small school of thought held that a high incidence of arterial sclerosis was related to large amounts of ultra-violet light linked with excess vitamin D. Ultra-violet light penetration was greater in pale than in dark skinned men, and white cattle suffered more greatly from fatigue in South Africa than did black cattle.

Dr E. J. Moynahan said that there was no doubt that melanin production formed an important part of the human protective mechanism against ultra-violet light. It had been shown that radiation of short wave-length stimulated melanoblasts to produce melanin and in addition ultra-violet light blackened pre-existing pigments in the skin. The melanin was laid down to begin with as a supra-nuclear cap in the cells of the malpighian layer of the skin. The thickness of the overlying hairy layer was another important factor affecting ultra-violet light penetration: this layer was thickened as a response to ultra-violet light, and was thicker in negroes than in the skins of white races. Neither a high intake of vitamin D nor excessive ultra-violet light played a part in causing arterio-sclerosis. The toxic effects of excess doses of calciferol were mainly confined to the kidneys and were reversible.

In answer to a question about the productivity of Sudanese cows, Dr Wright said that this was up to 1,000 gallons with an average of 350-400 gallons with good feeding. Butter fat was up to 8% with a normal figure of about 6%.

The Chairman asked Dr Bodil Schmidt-Nielsen whether she had examined the alveolar air of kangaroo-rats. She answered in the negative but said that the oxygen dissociation curve of these animals was the same as that of white rats, as was the oxygen and carbon dioxide content of the blood. In reply to another question she said that fat storage in the camel's hump and elsewhere had a negligable effect on water economy. The additional ventilation required for the oxidation of this fat counterbalanced the metabolic water produced.

Session VI

MAMMALIAN PHYSIOLOGY AND ECOLOGY II

Chairman Professor J. F. Danielli

Dr J. S. Weiner suggested that the discomfort zone might be higher than was thought, for people could tolerate a good deal of sweating without discomfort. The voluminous clothing of the Arabs kept out radiation and solar insulation, and saved water. When called on to do heavy work the Arab discarded most of his clothing. Little was known of the effect on Europeans of continuous residence in tropical climates.

Dr E. J. Moynahan said that there was a definite relationship between lack of pigmentation and the incidence of rodent ulcer and other cancers of the skin. These tumours occurred more frequently in white races living nearer the Equator. In mammals with protective coats of hair, cancers were very rare.

Mrs G. E. C. Stone emphasized the need for aerial surveys of deserts and especially of arid sub-desert marginal regions as a framework on which to fit detailed knowledge as it became available. Much geological survey work could be carried out by means of aerial photographs, a method that saved a considerable amount of time. At present photo-geologists concentrated on the areas in which oil and other minerals were likely to be found; but Professor Prescott had already said that in Australia water was considered the most important mineral. Photo-geological methods might indicate the direction of an aquifer, and the survey of desert marginal areas might assist protection against the extension of man-made deserts.

After the discussion, Dr Frank Malina spoke on behalf of UNESCO, and Professor J. F. Danielli, Honorary Secretary of the Institute of Biology, summed up. He said that from the papers presented at the symposium it was apparent that individual deserts presented a multitude of different problems. Scientific investigation must preceed development, but in most cases the major difficulties were social, moral and political and presented problems of ethics rather than of science.

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